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FOOD HABITS OF *FORMICA SUBNITENS* CREIGHTON (HYMENOPTERA: FORMICIDAE) AT WESTBANK, BRITISH COLUMBIA (1)

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The data presented in this paper were collected during the summer of 1955 at West-bank, British Columbia, in an attempt to determine the food of *Formica subnitens* Creighton. The life history and ecology and a detailed account of some of the factors that influence foraging of this ant were given in previous paper (Ayre, 1957, 1958 *a*).

METHODS.

The same nest and same census points for food sampling were used as in the foraging studies (Ayre, 1958 *a*). The method of sampling was as follows.

All solid food brought to the nest by the ants was collected during half an hour every hour throughout the period of ant activity on the days of study. Samples were taken on the same day as foraging was studied, i.e., fortnightly from May 11 to August 30. To compare the numbers of insects brought to the nest with the numbers of ants active on the trails, the food samples were taken immediately after the foraging observations, i.e., 15 minutes after each hour. The ants were prodded lightly with forceps and usually dropped the food, which was then removed. However, when the ants did not drop the food both the ants and the food were taken and the former destroyed. If the ants were picked up and the food forcibly removed they could not be allowed to return to the nest because they usually excited a large portion of the colony, so that activity was abnormal for five minutes or more. In contrast, the ants that dropped their food affected the others little.

The food collected each hour and from each trail was kept separate. Larvae were placed in 70 % alcohol, undamaged adults were pinned, and damaged specimens were placed in cotton batting in small tins. All insects were eventually identified as nearly as possible to species.

Data on collection of liquids by the ants were recorded in terms of the number of ants that returned to the nest with distended gasters. Observations indicated that these ants had fed on honey dew or other liquids. Undoubtedly ants that returned with only small quantities of liquid were frequently overlooked; hence the data presented on this portion of the diet are only approximate and minimum. These observations were made on each trail during three five-minute periods every four hours, from 4.00 a.m. until activity ceased, on one day every fortnight.

RESULTS

F. subnitens obtained food from two primary sources: animal tissues and liquids containing sugar. The former consited chiefly of insects that the ants captured and that were not objectionable to them. The liquids consisted of plant exudates and the excreta of Homoptera.

The insects captured and eaten were of many families. Their range in size was considerable: the smallest taken was approximately two millimetres long, and the largest, sphinx moth larvae, were approximately 50 millimetres long.

The ants attacked almost all the insects they encountered. However, not all those attacked were captured. Some with hard exoskeletons proved too well protected for the ants to capture, and others, such as adult Hymenoptera and Diptera, were too agile for the ants. Insects that feigned death after attack were usually released, as movement is apparently important in arousing and maintaining the predatory instincts of these ants. Other insects were unacceptable to the ants for various reasons. Coccinellidae and Chrysomelidae secreted liquids that were apparently offensive; immediately after seizing one of these insects the ants released their hold and cleaned their antennae and mouth parts. On several occasions dead Coccinellidae and Chrysomalidae were brought to the nest by the ants but, because these specimens were partially dry and badly damaged, they were probably dead when found. Setose larvae and the scaly adults of Lepidoptera were other groups of insects attacked but seldom captured by the ants; in both cases the ants usually abandoned their attack and cleaned their mouth parts.

In Laboratory studies, specimens of the chyrsomelid *Chrysolina gemellata* (Rossi) were offered to *F. subnitens* and, after repeated attacks by different ants, they were eventually killed and taken to the nest, but two days later they were all removed from the nest by the ants and examination with a low-power binocular microscope showed no trace of feeding.

Examples of insects not usually attacked by *F. subnitens* were myrmicophiles and insects that feigned death or were motionless when found by the ants. The setose larvae of the moth *Crambidia casta* (Pack.) were probably the most notable of the myrmicophiles. The relationships of this and other species of myrmicophiles with *F. subnitens* were discussed in a previous paper (Ayre, 1958a). Sometimes the ants walked over a motionless insect without showing any awareness of its presence. This occurred rather frequently with the strawberry root weevil, *Brachyrhinus ovatus* (L.), though this species was one of the largest sources of insect food.

F. subnitens is primarily a ground forager. It occasionally entered the soil in search of prey when there was a surface indication of food, e.g., the openings to another ant nest. Foraging on trees and shrubs was confined to those with aphid colonies tended by the ants. No foraging was observed on plants without aphid colonies. Hence soil-inhabiting and leaf-feeding

insects did not form a major part of the diet. Certain stages were not captured whereas other stages of the same species were. For example, the larvae of *B. ovatus* and the adults of noctuids were not taken as food though the adults and larvae, respectively, of these insects frequently occurred in the food samples.

There was great variation in the condition of the insects brought to the nest. Some specimens were in perfect condition whereas others were so badly damaged that they could not be identified other than as, e.g., larvae or adults. The condition of a specimen appeared to depend on the resistance it made after capture and on the degree of protection provided by its exoskeleton. Insects that offered resistance to capture were often damaged beyond recognition. Insects that offered little or no resistance were frequently brought to the nest while still alive and hence were usually in good condition and could be readily identified. Insects with tough exoskeletons, such as many beetles, were often found in apparently nearly perfect condition, despite the resistance they offered the ants. Some of the larger beetles remained in good condition after the ants had fed on them through a small opening they made between the sclerites on the ventral surface of the abdomen. The ants removed most of the contents of the body through the opening and left the exoskeleton intact.

The orders of insects taken as food and the total numbers taken by the colony during the observation periods, totalling approximately 3.5 % of the foraging time from May 1 to August 30, 1955, were: Hymenoptera, 535; Coleoptera, 250; Lepidoptera, 53; Diptera, 52; Homoptera, 55; Hemiptera, 38; Orthoptera, 45; others, 110.

Hymenoptera.—Approximately 93 % of the Hymenoptera taken as food were ants. These included *F. subnitens*, *F. subpolita* Mayr, *F. fusca* L., *Tapinoma sessile* (Say), *Lasius* sp., *Camponotus* sp., and *Aphaenogaster* spp. Some of *F. subnitens* undoubtedly were the dead from the same colony, as laboratory experiments indicated that the dead were always partly eaten before they were discarded. The major portion of the other species of ants were sexuals captured just before the nuptial flights, when males and females usually gathered around the nest openings and were readily captured by *F. subnitens*. Workers were taken throughout the year. On one occasion a nest of *F. fusca* was partially excavated by *F. subnitens* and all the larvae removed. These larvae were bitten and were liberally sprayed with formic acid, and from this it was assumed that all were intended as food rather than as slaves.

The only other species of Hymenoptera that could be identified was *Anomalon ejuncidum* Say, of an ichneumonid genus reported to be parasitic on the larvae of elaterids (Townes and Townes, 1951). Adults were seen feeding on the excreta of aphids tended by the ants. Specimens that appeared to be of *Apis* sp. were occasionally brought to the nest; however, identification was not possible, as no complete specimens were obtained.

Coleoptera.—The species of Coleoptera found most frequently in the food of *F. subnitens* was the strawberry root weevil, *B. ovatus*. This species comprised 16.4 % of the total of all insects taken from July to September and 12.7 % of the total from May to September. It was estimated that the ants destroyed seven per cent of the weevil population in the area, on a basis of 33 foot-square soil samples examined. A large number of those captured were teneral.

Four other species of beetles of which the adults were frequently captured by the ants were *Harpalus* spp., *Diplotaxis* sp., *Coniontis oblita* Csy., and *Phobetus comatus comatus* Lec. The first three were taken in small numbers throughout the season. The last was taken only in mid-May, immediately after emergence and while still teneral. *Rhynchites bicolor wickhami* Ckll., *Piosoma setosa* Lec., and *Dyslobius luteus* Horn were taken in only very small numbers. Very few larvae of Coleoptera were taken, and practically all these were of elaterids.

Lepidoptera.—Adults and setose larvae of Lepidoptera were seldom taken as food. Relatively naked larvae, however, comprised approximately four per cent of the total number of insects captured. Most of these larvae were 20 millimeters or more long and, as they had little unedible exoskeleton, they were consumed almost completely and thus they undoubtedly formed a far larger portion of the diet than is indicated by the numbers recorded. Noctuids were most numerous, but a few arctiids also were captured. The majority of lepidopterous larvae were taken in May and June; few were taken in July and August.

Diptera.—Practically all Diptera captured were of *Bibio albipennis hirtus* Lw., the adults of which occurred during the last week of May. The few other Diptera captured during the season were either teneral or so badly damaged that identification, even to family, was impossible.

Hemiptera and Homoptera.—The Hemiptera and Homoptera taken as food were a relatively heterogenous mixture of species with no one species or group predominating. The ants occasionally attacked the aphids that they tended but what caused this reaction was not determined. Adults of the membracid *Campylanchia latipes* Say, the nymphal stages of which supplied the ants with excreta, were frequently taken as food.

Orthoptera.—The chief orthopterous food was the hind legs of grasshoppers (possibly *Melanoplus* spp., the most common genus in the area). No complete specimens of adults were found and it is not known whether the legs were found by the ants or broken from the living insect during attacks by the ants. On one occasion the ants found a grasshopper egg case from which the newly hatched nymphs were emerging and quickly converged on the area and captured all the nymphs.

Others.—The only other insects captured in significant numbers were Mecoptera. All specimens captured were larvae; they could not be identified to species or genus.

The chief food other than insects was spiders. Various species of jumping spiders were often found near the nest during sexual flights, they were presumably attracted by the sexuals, on which they were observed to feed. They, in turn, were attacked by the ants.

The largest organisms taken as food were small tree toads, *Hyla regilla*
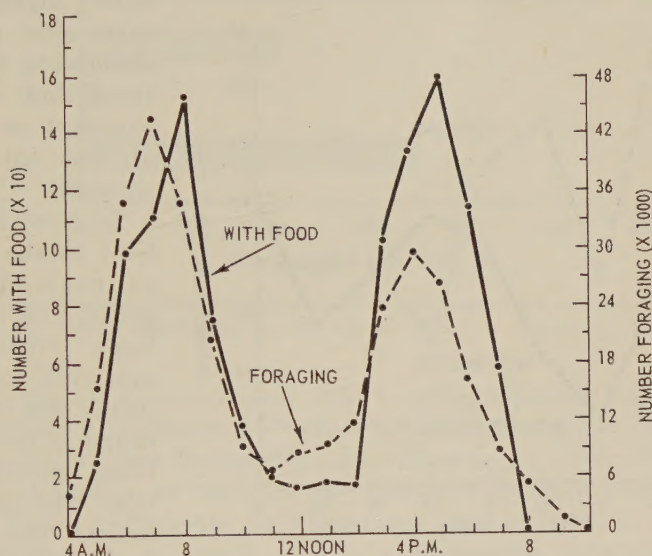
Fig. 1. — Numbers of *F. subnitens* with food and of those foraging; totals for hourly observations on one colony, May 1 to August 30, 1955.

Baird and Ger. Ants were not observed to attack and capture these under natural conditions. Controlled tests indicated that the toads are extremely sensitive to attack. Three ants were able to kill a toad. The toads were partially eaten in the field, as they were too large to be carried or dragged intact to the nest. Eventually, however, they were dismembered and various parts brought to the nest.

Bird faeces and the seeds of *Panicum* spp. and *Polygonum* spp. were miscellaneous items frequently brought to the nest. It is not clear whether these were used as food. *Polygonum* seeds and the husks of *Panicum* seeds were found incorporated in the thatch of the nest.

Figure I shows that the hourly food intake corresponded roughly with the numbers of ants foraging. Ants that find food when foraging are delayed in their return by both the attack on the prey and by having to carry or drag the prey to the nest. This explains why the peaks of food intake each occurred about an hour after a peak of foraging activity. The sudden rise in food intake at 2.00 p.m. and the resultant peak, which

was proportionately higher than the morning peak, followed a decrease in ant activity that resulted from high temperatures during the mid-day period. The ants did not return to the nest, but took shelter, when the temperatures that prevent or restrict ant activity were reached. Such temperatures were not reached in areas of heavy vegetation, where the ants continued to forage but did not return to the nest over the open areas until temperatures became more favourable. Because these ants accumulated food during the periods of high temperatures, there were proportionately higher food intakes after periods of unsuitable temperatures than would be expected on the basis of the ant activity recorded.

As shown in Figure 2 food intake was not proportional to ant activity on a seasonal basis. Observations indicated that food intake was associated more closely with brood development than with any other factor. The peak of food intake that occurred in May corresponded with the period immediately before pupation of the sexual brood. The relatively high level of food intake throughout July corresponded with the period of maximum worker brood development. The sudden increase in food intake at the end of August is not understood, unless the ants store food for use during the winter and early spring. If this is so, it may also explain the relatively low food intake during the first part of May though the ants rear a sexual brood at that time.

The discrepency between ant activity and food intake may be related to the relative availability of food in the foraging area. Brian (1953) showed that there is an optimum ratio of workers to larvae in the nests of *Myrmica rubra* L. If the same occurs with *F. subnitens* then the size of the colony determines the size of the brood, which in turn determines the food requirements of the colony. Therefore, any given colony requires a set amount of food, depending on the size of its brood. If protein food is scarce then it is likely that more ants are required for foraging than is necessary when food is plentiful.

Figure 3 shows the relative amount of food brought to the nest on each

FIG. 2. — Numbers of *F. subnitens* carrying food and of those foraging, May 11 to August 30, 1955.

foraging trail during the season.   However, examination of the monthly data showed that there was much variation in quantity of food per trail throughout the season.   There are two primary reasons for this: the availability of food in the area associated with each trail varied during the season; and the areas changed in their suitability for foraging by the ants. The latter seemed to be mainly governed by temperature: areas that were favourable for foraging in the spring became unsuitably hot and dry in the
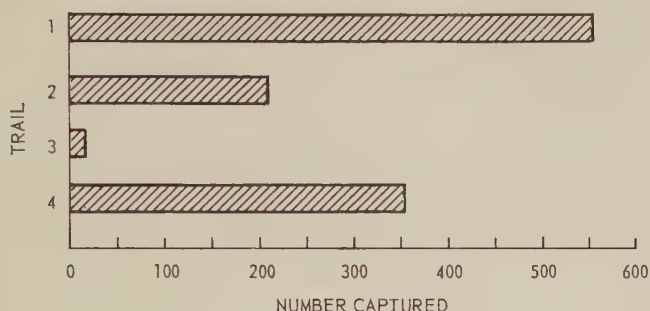
FIG. 3. — Relative numbers of insects captured by *F. subnitens* on the four foraging trails; totals for hourly observations on one colony, May 1 to August 30, 1955.

summer, when the ants restricted their foraging activities mainly to areas well protected by vegetation.   Further details of the factors that influence foraging activity were discussed in the earlier paper (Ayre, 1958b).

The liquid portion of the diet was normally obtained from two main sources.   The requirements of the colony appeared to be very small during spring and all liquid food was apparently obtained from the exudates of the young shoots and buds of *Pinus ponderosa* Laws.   The requirements of the ants for liquids apparently increased greatly in the summer, when the excreta of Homoptera was the chief liquid food.   Ten species of aphids and one species of membracid were tended by the ants (Table 1).   The relative importance of the aphids as a source of honey dew

TABLE I. — SPECIES OF HOMOPTERA USED BY *Formica subnitens* AS SOURCES OF LIQUID FOOD.

SPECIES.	HOST PLANT.
Cinara ponderosae Williams	*Pinus ponderosa* Laws.
Pentatrichopus tetrachodus Wlk.	*Rosa* sp.
Aphis maidi-radicis Forbes	roots of Compositae (poss. *Helianthus* sp.)
Moculolachnus rosae Cholod.	*Rosa* sp.
Neomyzus circumflexus Buck.	roots of a variety of plants
Bipersona torticauda Gill.	*Cirsium* sp.
Aphis helianthi Mon.	*Cirsium* sp.
Aphis gossypii Glov.	legumes
Cinara pseudotsuga Wils.	*Pseudotsuga menziesii* (Mirbel) Franco
Sappaphis plant ginea Pass.	*Malus* sp.

was discussed in a previous paper (Ayre, 1958b). Supplementary observations on other colonies of *F. subnitens* indicated that when the aphid colonies did not supply all the liquid food required, the ants bit the stems of succulent plants and collected the cell sap that exuded. This, however, appeared to be only a temporary occurrence, and as soon as the aphids became plentiful the ants abandoned collections of sap.

The gradual increase in the numbers of ants engaged in collecting honey dew (Figure 1) corresponded with the development of the worker brood in the nest. Eisner and Wilson (1957) found that very little carbohydrate liquid food, if any, was fed to larvae of the ants. Therefore the increase in liquid consumption by *F. subnitens* may have been caused by the needs of the callow worker ants, which are fed by the mature ants before they leave the nest to forage.

F. subnitens may not be particularly important as a control agent for any one species of beneficial or harmful insect. When the population of a prey insect increases the ants undoubtedly capture more specimens of that species but at the same time tend to capture relatively fewer of the other insect species in the area. The amount of food required by the ants depends on the size of the brood, which is relatively constant in terms of numbers of workers. Therefore, if a population of a prey increases, the area needed to capture a sufficient quantity decreases and consequently the foraging area decreases. It thus appears that these ants would be more effective in preventing than in controlling outbreaks of prey species.

The distribution of a population of a prey species is important in determining the number of individuals taken by ants. Green and Sullivan (1950) reported complete destruction of colonies of the forest tent caterpillar, *Malacosoma disstria* Hbn., by foraging *Camponotus herculeanus* (L.) and *Formica fusca* L. In this instance the gregarious nature of the caterpillars supplied a food source known to the ants, which continued to return to the area until the supply of food was exhausted. Non-gregarious prey insects, however, are not so prone to destruction by ants, as attack on any individual depends on a random meeting between it and ants.

F. subnitens did not establish aphid colonies, but accepted those that were available in the foraging area. Therefore, their influence on the vegetation of the area through the establishment of new aphid colonies may be negligible.

Summary.

At Westbank, British Columbia, the red ant *Formica subnitens* Creighton obtained food from two primary sources: animal tissues and liquids containing sugar. Animal tissues were of insects, and those that formed the largest part of the diet of the ants were other ants, Coleoptera, and Lepidoptera. Hemiptera, Homoptera, and Orthoptera were taken in lesser numbers. The number of insects captured per day varied depending on the number of ants foraging. The number captured throughout the summer varied with the requirements of the ant brood.

The ants used plant secretions from May to early June as a source of sugar. From June until September they collected honey dew from 10 species of aphids and one species of Membracidae.

Zusammenfassung.

Nach unseren Beobachtungen in Westbank, British Columbia, bezieht die rote Ameise, *Formica subnitens* Creighton, ihre Nahrung aus zwei Hauptquellen: Tierische Gewebe (Eiweissstoffe) und zuckerhaltige Flüssig-keiten (Kohlenhydrate). Die Eiweissstoffe erhält die Ameise durch ihre räuberische Tätigkeit von anderen Insekten, unter denen Formiciden, Coleopteren und Lepidopteren hauptsächlich vertreten sind. Ausserdem werden Hemipteren, Homopteren und Orthopteren in geringeren Mengen eingetragen. Die Zahl der an einem Tag erbeuteten Insekten ist von der Zahl der jagenden Ameisen direkt abhängig. Die Menge der während der Sommerzeit erbeuteten Insekten wird den Futteransprüchen der Brut angepasst.

Von Mai bis Anfang Juni dienen pflanzliche Ausscheidungen als Hauptquelle für ihren Bedarf an Kohlenhydraten. Ab Juni bis September sammeln die Ameisen Honigtau von 10 verschiedenen Lausarten und einer Membraciden-Art.

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THE FLIGHT ACTIVITIES AND COLONY-FOUNDING BEHAVIOR OF BOG ANTS IN SOUTHEASTERN MICHIGAN

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Introduction.

FLIGHTS AND COLONY-FOUNDING. — The activities of the sexual forms of ants during the flight season, and the manner in which the newly fertilized females establish their colonies are important aspects of ant ecology. Both processes contribute to the ecological distribution of ant species, and the flight behavior, in addition, affects the geographical distribution, the nuptial flights being the only active dispersal agency for most species of ants. In spite of the value of these two aspects of behavior and ecology, they have been largely neglected by North American myrmecologists. The relatively small number of recorded observations on flight activities are largely due to the keen observations of Mary Talbot (1943, 1945, 1948, 1956 ; also Talbot and Kennedy, 1940). She alone has studied the flight activities of ants as a process, and her work forms a foundation upon which comparative studies may be based. Knowledge of colony-founding behavior has advanced slowly since the summary of this subject by W. M. Wheeler (1933). Much work has recently taken place in Europe, and has largely been restricted to the social parasites. In recent years Eidmann (1931), Goetsch and Käthner (1937), Gösswald (1938), Hölldobler (1936, 1950, 1953), Kutter (1956), and Stärcke (1937) have studied colony-founding of species closely related to some North American bog-inhabiting ants. Information on the colony establishment process within bogs is almost completely lacking, and the behavior of few of the species that occur in this environment (as well as in other environments) has been described.

The observations herein recorded were obtained from May 1953 until September 1956 during a study of bog ant ecology in southeastern Michigan. Additional observations were made in the summer of 1957. I had hoped that knowledge of flight activities and colony-founding behavior would help explain the patterns of ecological distribution within this one environment. This objective was not fully realized during the course of the study mainly because of the large number (33) of species represented and because of the difficulties involved in observing flight activities. The flights of eight species were observed and, since these observations add significantly to our knowledge of this subject, they are here described in detail. I hope that these observations will provide a framework for future, more thorough studies on flight activities.

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DESCRIPTION OF THE STUDY AREAS. — The observations presented below were obtained at three bogs (1) : Hidden Lake (2) and Big Cassandra (2) bogs on the Edwin S. George Reserve, Livingston County, and Mud Lake Bog (2) in Webster Township, Washtenaw County, Michigan.   The parts of Livingston and Washtenaw counties in which the study areas are located lie within an area of morainal topography which varies in elevation from about 800 to 1,100 feet above sea level.   Lakes, bogs, swamps, and marshes are common in the lowlands in this region.   The soils of these bogs are usually peats and are acidic, except in marshy areas where a muck type of soil with a pH of approximately 7.0 generally prevails.

Big Cassandra Bog occupies a basin of approximately 15 acres that is surrounded by low hills which are largely covered by an oak-hickory forest.   This basin is now completely filled in, and is mainly occupied by dense growths of sphagnum and leather-leaf.   Two small "islands" of dead and living larches occur near the center of the bog.   Surrounding the leatherleaf community and separating it from the upland woods is a wet moat composed principally of grasses and sedges.

The Hidden Lake area includes a region of swamp, marsh, and bog mat that surrounds a small post-glacial lake remnant.   This lake is without inlet and outlet except for the indirect seepage that occurs through the swamp and for some water movement during the spring run off.   The bog mat is a narrow zone mostly 1 to 15 feet wide between the open water of the lake and the swamp forests, and is occupied primarily by a combination of mosses, sedges, ferns, cattails, and leatherleaf.   Most of the bog mat is encircled by an open swamp (larch swamp) composed of dead and living larch, poison sumac, dogwood, and other shrubs, and a surface layer of mosses and sedges.   Several small areas of deciduous hardwoods swamp forest are found between the bog mat and the upland, or between the larch swamp and the upland.   American elm, red maple, yellow birch, and other trees, 25 to 40 feet tall, are characteristic of the moderately open upper story.   Shrubs in this forest include poison sumac, holly, dogwood, etc., and the surface is characterized by ferns and more mesophytic mosses.   There are also certain marshy areas between the larch swamp and the upland forests which are occupied mainly by grasses, sedges, and ferns.

Mud Lake Bog occupies about 250 acres in sections 1 and 12 of Webster Township, Washtenaw County.   This bog includes a large complex of plant communities; however three distinct zones may be recognized: the bog mat, the subclimax forests, and the disclimax communities produced by fire.   The bog mat includes several communities of the pioneer stage of bog succession which are characterized by grasses, sedges, and ferns, and several consolidation communities which are composed principally of ericaceous shrubs and sphagnum mosses.   There are three major subclimax communities: a larch swamp, composed mainly of larch and poison sumac; a coniferous swamp forest dominated by black spruce; and a deciduous hardwoods swamp forest similar in flora to that of Hidden Lake Bog.   Fires have influenced the development of plant (and animal) communities in this bog. . The most recent one, in 1932 (Graham, 1956, p. 133), brought about the development of two disclimax communities: a heath-like area ("open-heath") with dense growths of blueberries and leatherleaf and a ground cover of mosses, principally sphagnum, which is now rapidly being crowded out by young larches and spruces; and a birch-aspen forest thickly populated by 15 to 25 foot high birches and aspens and with scattered patches of more mesophytic mosses on the surface.

(1) The word "bog" in this study is used in the broadest sense to include all present emergent and terrestrial communities which have developed as the result of a succession of plant growth in a single aquatic environment.   It therefore includes not only bog mats, but also swamp forests ans marshes which have developed in the same habitat.

(2) A brief description of each bog, sufficient for the purposes of this paper, is presented.   More detailed analyses of these environments and a description of the ecological distribution of the ants will be presented in a future paper.

METHODS. — Information on flight activities is difficult to obtain.   First, the time of the year that alates occur in the nests must be determined for each species.   Then, several mature colonies of each species must be observed at various hours of the day and under various climatic conditions to determine the approximate time of day at which flights occur.   When this information has been gathered, it is necessary to stake out several nearby nests and to visit them periodically to observe the flights and to record the climatic conditions.

Temperature readings were obtained at several positions. The temperature at a level approximately 8 cms. above the nest surface was recorded for all species.   This level gave a measure of uniformity in temperature comparisons among the several species.   The temperature inside the mounds and domes of species which inhabit these nest types was obtained whenever possible by using a Weston dial type thermometer.   In certain instances temperatures were recorded from the nest surfaces and at a height of approximately 30 cms. above the soil level.   Sky conditions were recorded as clear, partly cloudy, cloudy, and overcast.   Wind velocity was not measured because of the lack of special equipment; however, estimates were recorded as calm, slight breezes, moderate winds, and strong winds.   Illumination was measured with a Weston light meter and recorded in candles per square foot.   Relative humidity of the air just above the nest surface was obtained by means of a sling psychrometer and a Serdex meter.

TERMINOLOGY. — The following terms are introduced here as a means of facilitating later discussion.   Some of these are expressions that are already in general usage. Others have been created to cover types of behavior or conditions of activity for which terms are not presently available.

The time interval during which flights of a species occur in a given area is termed the *flight season*.   It extends from the date of the first flight to the date of the last flight of the season of this species.   The time of the day that flights of a species take place in a given area is the *flight period*.   The length of time for a flight from a single colony of a species in a given area is called the *flight duration*.

The term, *flight activities*, comprises all activities of an ant colony directly related to the flights of the sexual forms beginning with the preparations for the first flight and concluding with the termination of the last flight of each flight season.   Essentially, this is a continuous process which may be divided into three stages: pre-flight behavior, flight behavior, and post-flight behavior.   The activities leading up to a flight, such as the preparation of the nest, the activities of the workers in controlling the time of the flight, and the behavior of the alates in finding sites from which to fly, constitute the *pre-flight behavior*.   *Flight behavior* includes the means of becoming air-borne, the flight process, the magnitude of the flight, and the speed and direction of flight. The size of flights of different species apparently varies in a gradual and continuous scale from a few alates per nest per flight season to perhaps several hundred thousands. For convenience, flights may be grouped into three categories according to the average number of alates flying per minute for each flight.   *Sparse flights* are those in which the average rate of alates flying per minute is approximately two or less.   An average of 5 to 40 alates flying per minute is characteristic of *moderate flights*.   The large spectacular flights where the alates fly at an average rate of 100 to 1,000 or more per minute are considered *mass flights*.

Flights also vary according to the regularity of occurrence at individual colonies. Some species of ants have flights from each mature colony regularly day after day (unless extreme climatic conditions—usually rain—interfere) from shortly after the first alates mature until the last have flown.   These are termed *continuous flights*. Other species have flight behaviors in which the flights are spread over many days and (in the absence of unfavorable conditions) probably take place in the area daily, but not from each mature colony.   Such flights are referred to as *discontinuous flights*. In certain other species no flights occur until most, if not all, the alates have matured. These flights usually occur over one or several short periods of time with alates flying

from most colonies on the same days.   Flights of this type are called *accumulated flights.*

The actions of the alates immediately after returning to the ground constitute the *post-flight behavior.*   The activities of the males, the dealation processes of the females, and the microhabitat selection process by the females are essential features of this post-flight behavior.

Mating behavior refers to those activities directly concerned with mating including the attraction of the males to the females and the actual process of copulation. Mating may take place before, during, or after a flight, or it may take place in the absence of flights.

After copulation the newly fertilized female begins the process of finding or making a nest for her offspring.   This process is termed the *colony-founding behavior.*   There are two main types of colony-founding: *independent*, in which the female establishes her colony without any assistance; and *dependent*, in which the female requires the assistance of workers from a previously existing colony of ants.   Two distinct patterns of behavior of the females in the independent process may be distinguished: 1) *claustral behavior:* the female forms a brood chamber with the external opening sealed shut so that she must remain in the chamber continuously until the brood has matured; 2) *non-claustral behavior:* the female forms a brood chamber which has an external opening, permitting the female to forage for food while her eggs develop.

Two general methods of dependent colony-founding are known: colony division and social parasitism.   *Colony division* is the process by which a part of an existing colony separates from the remainder of the colony and begins an independent existence.   *Social parasitism* is the condition whereby the colony-founding female utilizes an existing colony of ants to care for her and bring up her brood.   In most ant species exhibiting social parasitism the colony-founding female enters a colony of an ant species whose own colony was established by the independent process.   Some social parasites, however, invade colonies of other social parasites and are thus termed *social hyperparasites.*

OBSERVATIONS

My observations are recorded below by species.   The scientific names of the ants are generally based upon Creighton (1950).   However, several departures from Creighton's usage have been made for which I take full responsibility.   Justification of these changes is deferred to a future paper.

The time of occurrence of alates in nests is poorly known for most species of ants.   Published records are cited below only for regions adjacent to southeastern Michigan, except where adequate information is available for most of the range of the species.   The period of time during which alates were found in the colonies is shown in Table I.   Table II summarizes the conditions under which flights took place.   The methods of colony-founding utilized by bog ants are presented in Table III; the nest sites occupied in this process are listed in Table IV.

PONERA PENNSYLVANICA Buckley.   Alates were present in nests from August 6 to September 26, but absent in spring months indicating that flights occur in the fall.   This correlates well with the observations by Headley (1943a, p. 24; 1952, pp. 438, 439) of alates in nests

TABLE I. — PERIODS OF ALATE OCCURRENCE IN NESTS OF BOG ANTS IN SOUTHEASTERN MICHIGAN.

SPECIES.	JUNE.	JULY.	AUGUST.	SEP-TEMBER.	OTHER MONTHS.
Ponera pennsylvanica Buckley			———	———	
Myrmica brevinodis Emery		———			
Myrmica emeryana Forel		———	———		
Myrmica fracticornis Emery	———	———			
Myrmica punctiventris Roger			×		
Myrmica Species "A"					
Leptothorax ambiguus Emery		———			
Leptothorax curvispinosus Mayr	———	———			
Leptothorax duloticus Wesson			×		
Leptothorax longispinosus Mayr			×		
Leptothorax muscorum Nylander		———			
Crematogaster cerasi Fitch		×			
Tapinoma sessile Say	———	———			
Dolichoderus mariae Forel			———	———	
Dolichoderus plagiatus Mayr			———		
Dolichoderus pustulatus Mayr		———	———	———	
Camponotus nearcticus Emery				———	October through May
Camponotus noveboracensis Fitch	—		———	———	October through May
Lasius alienus Foerster			×		
Lasius minutus Emery		———	———	———	
Lasius speculiventris Emery		———	———		
Formica fusca Linnaeus	———	———			
Formica neorufibarbis Emery		×			

TABLE II. — SUMMARY OF CONDITIONS UNDER WHICH FLIGHTS IN BOGS TOOK PLACE.

SPECIES.	FLIGHT SEASON.	FLIGHT PERIOD.	TEMPER-ATURE (Fahrenheit).	RELATIVE HUMI-DITY.
Myrmica fracticornis Emery	July 17-Aug. 6	6:00-7:30 PM	65°-78°	50-76 %
Tapinoma sessile Say	June 26-July 14	8:20 AM-1:15 PM	67°-83°	29-84 %
Dolichoderus mariae Forel	Aug. 11-Sept. 9	6:15-9:30 AM	56°-78°	68-95 %
Dolichoderus plagiatus Mayr	August 11	8:00-8:10 AM	66°	90 %
Dolichoderus pustulatus Mayr	August 9-20	7:15-9:30 AM	63°-75°	72-93 %
Lasius minutus Emery	Aug. 18-Sept. 9	2:00-5:30 PM	70°-84°	71-89 %
Lasius speculiventris Emery	Aug. 27-Sept. 9	2:35-5:15 PM	77°-85°	75-89 %
Formica fusca Linnaeus	August 2	8:40-9:30 AM	69°-75°	75-83 %

TABLE III. — METHODS OF COLONY-FOUNDING OF BOG ANTS IN SOUTHEASTERN MICHIGAN

SPECIES.	INDEPENDANT.		DEPENDENT.		
	Claus-tral.	Non-Claus-tral.	Colony Divi-sion.	Social Par-asitism.	Host in Bogs.
Ponera pennsylvanica Buckley		×			
Myrmica brevinodis Emery		×			
Myrmica emeryana Forel		×			
Myrmica fracticornis Emery		×			
Myrmica puncticentris Roger		×			
Stenamma diecki Emery		?			
Leptothorax ambiguus Emery	×				
Leptothorax duloticus Wesson				×	Leptothorax ambiguus
Crematogaster cerasi Fitch	×				
Tapinoma sessile Say	×				
Dolichoderus mariae Forel		?			
Dolichoderus plagiatus Mayr		×			
Dolichoderus pustulatus Mayr		×			
Camponotus nearcticus Emery	×				
Camponotus noveboracensis Fitch	×				
Lasius alienus Foerster	×				
Lasius minutus Emery			?	?	? Lasius alienus
Lasius speculiventris Emery			?	×	Lasius minutus
Lasius umbratus Nylander	×				
Formica fusca Linnaeus	×				
Formica neorufibarbis Emery	×				
Formica ulkei Emery				×	Formica fusca

TABLE IV. — NEST SITES UTILIZED BY BOG ANTS IN INDEPENDENT COLONY-FOUNDING.

SPECIES.	CURLED LEAVES.	HOLLO STEMS.	SOIL CHAMBERS.	WOOD CHAMBERS.
Ponera pennsylvanica Buckley	×		?	
Myrmica brevinodis Emery	×		×	×
Myrmica emeryana Forel			×	
Myrmica fracticornis Emery	×		×	
Myrmica puncticentris Roger			×	×
Stenamma diecki Emery			×	
Leptothorax ambiguus Emery	×	×	×	
Crematogaster cerasi Fitch		×		
Tapinoma sessile Say	×	×		
Dolichoderus mariae Forel	?		?	
Dolichoderus plagiatus Mayr	×			
Dolichoderus pustulatus Mayr	×	×		
Camponotus nearcticus Emery		×		?
Camponotus noveboracensis Fitch			×	×
Lasius alienus Foerster	×	×	×	×
Lasius umbratus Nylander			×	
Formica fusca Linnaeus			×	
Formica neorufibarbis Emery				

in upland communities in northeastern Ohio during late summer and early fall. Flights at Ithaca, New York were observed by Haskins and Enzmann (1938, p. 154), but they did not indicate the date and time.

An alate female was found crawling on the sphagnum surface of the leatherleaf community at Mud Lake at 1:50 PM on September 26, 1954. She may have just dropped after a flight about midday. Additional evidence that alates fly at this time of the year was obtained when alate females were collected in flight at 2:00 PM on September 15, 1955 in a yard in Ann Arbor, Michigan.

MYRMICA BREVINODIS Emery. Alates were found in nests between July 20 and August 14. In most *brevinodis* nests examined after the middle of August alates were absent, but some were present in two of three colonies which I examined on October 13, 1955. One of these colonies had only a few alate females; the other had several males as well as alate females. These two instances were probably the result of delayed development; these alates likely would never have flown. They might have mated within the nest. The females may have remained there either to increase the number of queens or else to leave the nest the following spring to establish new colonies. The fact that the females still had wings implies, however, that they probably had not mated.

Colonies of *brevinodis* in these bogs were always started in a moist environment, and were usually established by solitary dealate females in closed chambers in the soil, a curled leaf, or a cavity in a piece of wood. However, one incipient colony was found in a soil nest in which two queens were present.

MYRMICA EMERYANA Forel[3]. Nests of this species were found to contain alates between August 7 and August 28, suggesting that flights occur in late summer. None have been seen, however.

Flights of an ant determined as *emeryana* from nests in a yard in north-central Ohio have been recorded by Talbot (1945). Her observations showed that these flights usually occur from 6:00 to 8:00 AM in mid—and late July. However, because of certain morphological, ecological, and behavioral differences, it is not certain that the Ohio population studied by Talbot and the Michigan bog population here considered are conspecific.

MYRMICA FRACTICORNIS Emery. Alates were present in nests between July 5 and August 16. Eight colonies of this species, all known to contain alates, were located and marked in Big Cassandra in July, 1956. These nests were watched from 3:30 to 8:00PM at intervals of two or three days over a two week period, and from 5:30 to 9:30 AM on several mornings. Flight activities were observed on seven days between

(3) This determination is based upon the work of Creighton (1950) and Weber (1947). The identification is questionable because of the possibility that there may be more than one species population presently existing under this name.

July 22 and August 6.   In the summer of 1957 evening flights were observ-
ed from three colonies (a different colony each evening) on July 17, 18,
and 19.

In 1956 alates were first noted outside of the nests on July 22.   A few
alate females came out of one nest at 3:30 PM and crawled over the moss
and up the moss sporangia and the low stems of leatherleaf a few inches
from the nest entrance.   Within one to three minutes all alates one by
one returned to the nest.   For five minutes there were no alates out of
the nest.   Then one by one a few alate females again came out of the
nest, crawled on the moss and up and down the leatherleaf stems as
before, and again, after a few minutes, they returned to the nest.   This
performance was continued without any interference from the workers
until 6:45 PM when all activity ceased.   The number of alates present
outside of the nest varied from two to five; all were females.   Throughout
the day none of the alates ever fluttered their wings or made any attempt
to fly, perhaps because of the moderately strong winds that day.   Their
behavior could not be correlated with sunlight or temperature.   Perhaps
they responded to warning sounds made by one of them.   There appeared
to be no influence on their activities by the workers.   No activity was
noted at any other nest.

On July 23, the alates first appeared outside of this same nest at 3:45 PM.
The same type of activity described above continued until about 6:00 PM
with only one unusual feature.   At 5:11 PM a dealate female came out
and crawled about 25 centimeters away from the entrance, where it was
overtaken by an alate female.   The latter grasped with her mandibles
one antenna of the dealate female and towed her back to the nest.   No
dealate female was seen outside of the nest again on this evening.   Until
6:00 PM the number of alates seen out of this nest and two others varied
from one to six per nest; none had flown.   After 6:00 PM the number of
alates increased to 12 to 15 per nest, several of them flying.   Flights
ceased shortly after 7:00 PM, but the alates remained on the vegetation
and nest surface until 7:45 PM.

Behavior similar to that just described was noted on other afternoons
and evenings, indicating that there is a pre-flight adaptation in this
species.   The greatest period of activity, both in number of nests involved
and in number of alates occurring outside the nests, is from 6:00 to 7:30 PM,
at temperatures varying from 78° to 65° F.   All flights in the evening
occurred within these times and temperature ranges.   Within a certain
temperature range, the activities of alates seemed to increase with
decreasing light intensity until a certain minimum threshold was reached
about 15-20 minutes before sunset.

In order to determine whether *fracticornis* may also show early morning
flight activity, the same nests discussed above were watched on several
mornings.   Only 5 alates were seen out of the nests in the mornings
(between 6:30 and 8:30); three of these were seen to fly; the other two
were lost and probably flew.   On the basis of these observations it seems

likely that flights take place principally in the evenings, but that individual alates may fly in the morning. Temperature and light conditions at these two times are similar except that in the evening the light intensity and temperature are decreasing, in the morning, increasing. *Myrmica fracticornis* seems to be adapted to undertake flights primarily under conditions of decreasing temperature and illumination.

Flights of *fracticornis* are unspectacular considering the number of colonies present in the open communities of the bogs. Inasmuch as 100 or more alates may be produced by each mature colony, the lack of large conspicuous flights in these areas must be the result of many sparse flights, which evidently take place from a given nest at intervals and from different nests at different times. Probably alates fly soon after they mature. Of the eight colonies observed, flights were seen to occur from only three, although alates were known to be present in all eight. Probably the other colonies had flights on days when observations were not made.

The alates flew singly; there were no large numbers of them flying at the same time. Among those that flew in the evening, there was a considerable amount of maneuvering on the stems and leaves of leather-leaf for the best position from which to fly. All alates seen to fly in the morning flew without hesitation. There was no fluttering of the wings prior to flight. Each alate released its hold on the stem or leaf on the first stroke of the wings, and flew upward at approximately a 60° angle, rising high into the sky until lost from view.

Some mating probably takes place in the air. However, some mating evidently also occurs in the nests. I found shed wings in nests on several occasions, and the dealate female observed leaving the nest on the afternoon of July 23 was probably one that had mated in the nest. Additional evidence of intranidal mating came during the early morning observations. On the mornings of July 27 and August 2, dealate females were seen crawling out of three of the study nests, including one from which no flights were seen. At least 14 dealate females and one that was partially dealate left one nest on July 27. All of these females left the nests independently (rarely more than one or two were out near a nest at the same time) between 6:30 and 8:30 AM. All crawled over the moss surface, rarely climbing any of the shrubs. The several that were watched until they had stopped moving were found to have traveled from three to eight feet from the nest. Each examined the moss surface carefully, trying to enter small crevices, etc. All finally settled in small spaces in living *Polytrichum* and spagnum moss. None of these females was later found in the same place, so that it is suspected that each female may spend considerable time in locating a permanent nest site.

Considerable variation in brood production and development was noted in incipient colonies. In late summer and fall some colonies were found to contain eggs and larvae, while others consisted only of the founding female. Besides the female only larvae were overwintered.

Typically, the brood chamber formed by a colony-founding female was about 12 mm. long by 8-9 mm. wide and high. When completed, the walls were rather smooth-surfaced, and the entire chamber was free of debris. The nest entrance, although obscurely located, was always open or only lightly covered by surface debris.

MYRMICA PUNCTIVENTRIS Emery. Alates were found in colonies on August 13, 1957. The presence of immature pupae of the alate forms in several colonies at this time suggests that alates probably develop until about the first of September.

MYRMICA species "A"[4]. Alates of this species were found in bog nests between July 24 and September 2. Flights probably occur in August and early September, but none have been observed.

LEPTOTHORAX AMBIGUUS Emery. Alates were found in nests between July 9 and August 29, but were seldom numerous. This condition plus the fact that the pupae of the alate forms were found for 3 to 4 weeks after the first alates have appeared suggests that alates fly very soon after maturing, probably remaining in the nest only for a few days to complete the maturation process.

Flights probably occur in late July and August, but none were seen. What may have been a prelude to a flight was observed about noon on July 26, 1954 at Mud Lake Bog. Alates of both sexes were crawling on sedge stems and on moss near a nest, but did not fly. Many workers were active among the alates; they did not, however, deter the alates from their activities. At the time of this activity the nest was largely shaded and the temperature was 85° F.

The female starts her colony in a variety of situations (Table IV). Chambers that are formed between two leaves, especially leatherleaf leaves, are often altered by the addition of a salivary secretion to the edges of the leaves so that they stick together. All nests of the colony-founding females are without apparent openings, all previously occurring openings being partly or completely filled with bits of debris.

LEPTOTHORAX CURVISPINOSUS Mayr. Alates were found in nests in bog communities from July 7 to August 6. In upland forest communities on the George Reserve, where *curvispinosus* is common, Talbot (1957, p. 451) found that alates were present in nests from late June to early August.

LEPTOTHORAX DULOTICUS Wesson. The single colony of the slave-making ant, *Leptothorax duloticus*, found with *L. ambiguus* as the

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(4) This appears to represent a distinct species to which a name cannot be applied with certainty at this time.

slave, contained male pupae when collected on July 23, 1954. By the first of August only one male had emerged from its pupal integument; when it was preserved on August 12, it had fully matured. None of the other pupae survived. Talbot (1957, Table II) has determined that alates of this species occur from late July to early September in nests in upland communities on the George Reserve.

LEPTOTHORAX LONGISPINOSUS Mayr. Headley (1943b, Table I) in a population analysis of this species in a woods in northern Ohio, found alates in nests on July 12 and August 16, 1942. The single record of alates in the bogs came on August 12, indicating that the period of alate occurrence in southern Michigan bogs may be slightly later than for upland communities in Ohio.

LEPTOTHORAX MUSCORUM (Nylander). Alates were found in nests from July 26 to August 7. Because pupae of the alate forms were abundant in several nests on August 7, 1956, it is probable that alates may sometimes occur in nests to middle or late August.

CREMATOGASTER CERASI (Fitch). Males were collected on July 21, 1953, and pupae of the alate forms were found in nests from July 16 to August 26. Flights probably take place between late July and early September. Gaige (1914, p. 9) found alate females of this ant in nests in late September on the Charity Islands, Michigan.

Colonies are established in preformed cavities. A female found in a small chamber in a hollow flowering stem of a pitcher plant was still alate on October 20; no brood was present. Both ends of the chamber were closed by walls of plant fragments, indicating that *cerasi* colonies are clearly claustral. An incipient colony found in a 13 centimeter long section of a hollow flowering stem of *Scirpus cyperinus* on August 6 consisted of a queen, 11 workers, 4 worker pupae, 25 larvae, and 28 eggs. This was probably a first year colony in which all the workers and brood had developed from eggs laid in the spring and early summer. The workers of this collection were of small size, and many were callow. No mature colonies, i.e., those with alates, were found in the hollow stems. Evidently, the colonies move from the hollow stems to stumps, logs, or other types of wood when they outgrow their quarters. A mature colony containing males found nesting in chambers in a sphagnum hummock on Big Cassandra Bog in late July may have originated in a hollow stem and later moved into a hummock. This nest was located in a part of the bog in which no wood was present, which probably accounts for the unusual nest site. No colonies have been observed in the act of moving from one nest to another in the bogs. However, I have noted this behavior several times in colonies in upland forest communities at the University of Michigan. Biological Station in Cheboygan County, Michigan, and at the Harwood Reserve, Section 2, White Pigeon Township, St. Joseph County, Michigan.

TAPINOMA SESSILE (Say). The sexual forms of this ant were found in bog nests from June 26 to July 15. Alates have been recorded by Smith (1928, p. 313) as occurring in nests from June 10 to July 9, presumably in upland communities in the Champain-Urbana area in Illinois. Gaige (1916, pp. 2-3) reported alates in nests on July 9, 1914 in Chippewa County, Michigan.

Flights were observed from nests at Big Cassandra on June 29, 1954 and on eleven days between June 26 and July 14, 1957. In the latter
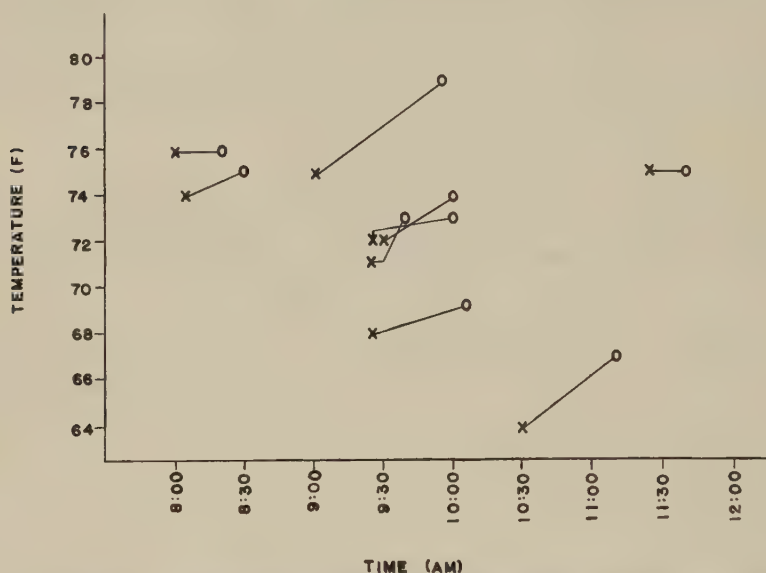
Fig. 1. — Correlation of temperature and time of flight activities of *Tapinoma sessile* (Say) from a nest at Big Cassandra Bog, E. S. George Reserve, Michigan in June and July, 1957. X=emergence of alates from the nest; O=beginning of flight.

summer the nests were watched every day from June 26 to July 7; flights occurred each day except June 27 and 28, when inclement weather prevented any activity. Alates usually left the nests about mid-morning, the earliest record being 8:05 AM and the latest, 11:15 AM (Fig. 1). Flights took place within 15 to 55 minutes after the alates first emerged from the nests, with an average range of 35 minutes. The earliest flights commenced at 8:20 AM while the latest starting time for a flight was at 11:40 AM. This latter flight was delayed because of an early morning rain. Usually the flight duration was one to one and one-half hours. The latest time for the termination of a flight was at 1:15 PM. Thus, the flight period extends from 8:20 AM to 1:15 PM in this bog.

Alates first emerged from the nests at temperatures varying from 64° to 76° F. Flights commenced at temperatures varying from 67° to 79° F. The maximum temperature recorded during a flight was 83° F. The time and temperature at which alates first left the nests and at which the alates

first flew have been correlated in Fig. 1. It is evident from the figure that alates become active and fly earlier in the day if the morning temperatures are warm, evidently above 72° F. Cooler temperatures delay activities until later in the morning. However, direct sunlight affects the flight activities (see below), and this factor has not been considered in the figure.

Relative humidity during the time that alates were out of the nests ranged from 84 % to 29 % with the highest readings early in the day when the alates first emerged from the nests and the lowest readings at or near the end of a flight. Thus, the relative humidity decreased during the period of flight activities each day. Except that extremely high humidities might possibly have prevented flight activities (something that was not clearly evident during observations), it seemed that flights took place independent of the relative humidity.

With one exception, winds during the flight period were moderate or less, and appeared not to affect the flights. Gusts of winds caused the temporary cessation of flights on one day. At this time the alates retained their positions on the vegetation and did not return to the nests. However, flights were renewed during the short (10 to 30 second) intervals between gusts.

The sky during flights varied from clear to overcast. An absence of flights was noted on cloudy days, if the temperatures were below approximately 70° F. The occurrence of flights on clear to partly cloudy days with temperatures as low as or even lower than this indicates that direct sunlight warms the nests and alates and makes possible flights at cooler temperatures. The presence of sunlight seemed to have no effect on the emergence and subsequent flights of the alates, if the early morning temperatures were above 72° F. With early morning temperatures of 72° F. or less, the alates usually began their activities only after direct sunlight had reached the nests. Evidently, sunlight under these conditions brings about the initiation of flight activities by warming the nests. The minimum light intensity for commencement of flight activities was about 200 candles per square foot. High light intensities (above 1600 candles per square foot) seemed not to affect the flights adversely.

The bog nests of *sessile* are rather inconspicuous. The several entrances are usually located beside stems emerging from the moss. Prior to the beginning of flights a number of new openings were created beside stems and openly on the surface. Most of these latter entrances were closed off after the flight season.

When both sexes were present in the nests, males were usually the first to leave the entrances on a flight day. Workers always preceded the alates. Some workers would move rapidly out onto the shrubbery, while others would retain the alates within the nest. The workers on the shrubbery moved rapidly back and forth on the stems. They may have functioned in forming odor trails, but it seemed from their behavior that they were more concerned with finding other organisms on the shrubbery.

After 5 to 20 minutes of this behavior, the workers at the entrances started admitting the alates to the shrubbery. The alates then moved rapidly over the branches, their actions being similar to those of the workers. Upon coming to the end of a stem or leaf the alates stopped and briefly examined the site. However, if touched by another alate or by a worker, the alate immediately moved off the site. Workers, which were constantly moving over the shrubbery, seemed not to leave the alates alone, but quickly moved up to the nearest alate and touched it with the antennæ, thus stimulating the alate to move. This worker activity definitely kept the alates on the move and seemed to be directed toward forcing the alates to fly immediately—something that the alates seldom appeared ready to do. The continual activity of the workers did force the alates to fly, but it also caused the alates to waste considerable time in moving from place to place because they seemed not ready for flight. This worker activity repeated every day during the flights seemed more to prolong the flights than to shorten them.

Alates almost always flew the stems and leaves of the shrubbery by the nest. On days of heavy flights some alates would fly from the ground.

Sometimes the alates would flutter their wings prior to flight, but fluttering was not a characteristic feature of the flight process. Prior to flight the alate typically held on to the leaf with all legs. Then it would often raise the front pair of legs and the front part of the body. The alate would release its hold on the leaf during the first stroke of the wings, and would quickly rise into the air. The angle of flight varied from about 15º to almost 90º from the horizontal, but was most frequently in the range of 45º to 75º. Alates flew in all directions from the nests, sometimes circling. However, on several days most of alates seemed to fly off in certain directions. On one clear day and on one partly cloudy day most flights were to the southeast. On another partly cloudy day most flights were toward the northeast. It was evident, however, that the alates seldom flew directly towards the sun, but seemed most often to move to the right or left of it. The flight was usually between 3 and 6 feet per second, although speeds estimated at 10 feet per second were occasionally noted on warm days. Males were swifter fliers than the females.

In general, the flight size for *sessile* is moderate. Usually from 100 to 1000 alates would fly from a nest on a day at a rate of 10 to 50 per minute. However, much depended upon the size of the colony. One small colony under observation seldom mustered more than 30 to 50 alates per day, and these would fly over an hour-long period. On the other hand, one large colony usually had flights of one to several thousand alates over the same length of time. It was estimated that more than 10,000 alates were seen to fly from this one nest in 1957.

The sex ratio of alates varied considerably from nest to nest. One colony apparently produced only females. All of the others produced both sexes, but with the males apparently always in excess, and usually greatly so. The early flights were almost entirely male, with ratios

estimated at about 50 to 1. Later, females were proportionately more abundant, and on one day at one nest females actually outnumbered the males. During the entire flight season, it seemed that about 10 males flew for every female. However, it is believed that the ratio of males to females developed in the colonies is not so high, and that not all of these females actually take flight (see below).

Near the end of a flight some workers would keep additional alates from leaving the openings, and other workers on the shrubbery would increase their activity—first in forcing the alates to fly, and later in getting those that had not flown to return to the nest. This clean-up operation by the workers would usually last about 10 to 15 minutes barring any breaks out of the nest by alates. Shortly after the last alates had returned to the nest, the shrubbery and surface by the nest gave little evidence of ant activity by *sessile*.

Smith (1928, pp. 313-314) presents evidence which clearly indicates that some mating takes place in nests, the many newly dealated females remaining in the nest. This behavior was confirmed repeatedly in the bogs by finding dealate females leaving the nests during the flights, and by finding large numbers of dealate females and of shed wings in the nests during the flight period. Wheeler (cited by Smith, 1928, p. 314) determined that the females start their colonies independently. In the bogs colony-founding females and incipient colonies were frequently encountered in mid—and late summer. All colonies were established in hollow stems or curled leaves. No brood was found with any of these females until late July; by the end of summer a few workers had usually been developed. However, several nests were found in late fall in which neither brood nor workers were present in the chambers.

As Smith (1928, p. 320) has reported, nests are seldom permanent. Even some of the large mature colonies in the bogs moved about from year to year. The nests in hollow stems are probably used only until they can no longer accomodate the growing colony. At this time the colony likely forms a new nest in the soil, for no mature colonies were found in hollow stem nests. Nests in curled leaves are more adaptable since the colony has only to add living space in the soil or debris under the leaves.

DOLICHODERUS MARIAE Forel. Alates were found in bog nests between August 9 and September 9. Flights occur daily from early or mid-August to mid-September.

The flight activities of this species were observed at nests at both Big Cassandra and Mud Lake bogs in 1954, and again at Big Cassandra in 1956 and 1957. Concurrently with my observations of the flights from the bog nests in 1954, Mary Talbot was observing the flights from a *mariae* nest in an upland community on the George Reserve (Talbot, 1956). Eighteen flights were watched in the bogs in 1954, while seven flights were seen in 1956 and two in 1957. In 1954 alates were first seen on the nest

surface at Big Cassandra on August 9. Examination of this colony on August 4 disclosed that alates had not yet matured, so that the first alates must have appeared sometime between August 4 and 9. The first flights were observed on August 13, 1954. It is not known whether flights took place prior to that day in 1954.

In the summer of 1956 the nest at Big Cassandra was observed daily from the first of August until August 21. Callow alates were first found in the nest on August 13, and the first alates appeared on the nest surface the following day. No flights occurred, however, until August 21. Thus, there is approximately a one week interval when the alates are present but do not fly. Presumably, this length of time is required for the maturation process to be completed, and/or for the population of alates to increase to a size large enough to cause the initiation of the flights. Because the climatic conditions at this time are similar to those later in the month when flights occurred, it appears that climatic factors may not be important in initiating the flights. The earliest record of a flight was obtained on August 11, 1957; however, it is believed that flights occurred prior to this day in 1957. Once the flights commenced, they took place daily until the last alate had matured and flown in September. The last flight day in 1954 was September 7; alates were still flying and pupae of the sexual forms were still present in nests on September 9, 1956 when the last observation was made for that year. I believe that in most years the flights would have ended sometime between September 5 and 15.

Prior to the beginning of the flight period the newly emerged alates perambulate briefly on the nest surface at various times of the day, but most frequently in the morning. This curious behavior of the alates, aimlessly moving over the nest surface and crawling in an out of the nest, but never or very rarely ascending any of the branches and stems of leatherleaf which grow through the nest, continues throughout the flight season after each daily flight is completed. Near the end of a day's flight some of the alates would crawl back down the branches and onto the nest surface. There seemed to be no interference by the workers of the nest, and usually the alates returned to the nest of their own accord. Some of them would parade on the nest surface and go in and out of the nest. In 1954 such parades were seen on both nests after every flight except the last. Alates which did not take part in the morning's flight also came out on the surface. A parade of 5 to 30 alates in addition to many workers was usual, occurring intermittently throughout most of the mornings and often in the afternoons as well. This behavior is probably a part of the maturation of the alates. It may contribute to drying after emergence from the pupal integument and may also be a form of exercise in preparation for flight on the following day. Logier (1923, p. 248) apparently first noted this same phenomenon on nests of the closely related species, *D. taschenbergi* (Mayr).

Once the flights have begun, it seems evident that the alates fly within two to four days after they have emerged from the pupal integument.

Sampling of the population of the colony on Big Cassandra during the flight season indicated the presence within the nest of about 1000-1500 mature alates at any given day. This number of alates would normally fly in about 1-4 days. Callow alates were found in nests, but were never seen on the surface. It may be usual for an alate to emerge on one day and stay in the nest as a callow that day and possibly the next, to take part in the parade on the second or third day, and to fly on the third or fourth day.

Flights always occurred early in the morning, all records falling between 6:15 and 9:30 AM. The time when the flight started each day depended upon the temperature. If the night had been moderately warm (the early morning low temperature higher than 61º-62º F.), the alates would fly early. i.e., from 6:15 to 8:00 AM; if the night had been cool (the early morning low below 61º-62º F.), the workers and alates remained in the nest until it was reached by the first rays of sunlight. This appeared to warm up the nest so that within several minutes the workers and alates began to emerge. The nest on Big Cassandra was located in the southeastern corner of the bog. At the beginning of the flight season it was shaded by the trees of the upland forest until approximately 7:30 AM, toward the end of this period until approximately 7:50 AM. The nest at Mud Lake was situated in a more open area; the bog forest was to the northeast of the nest and shaded it only until approximately 7:00 to 7:15 AM during the last 10 days of August and the first week in September. Flights occurring at approximately the same time of the month and under similar climatic conditions appeared to take place slightly earlier in the morning at Mud Lake than at Big Cassandra.

Flights occurred when the air temperature three inches above the moss surface was between 56º and 78º F., and most of them in the range between 63º and 69º F. With initial temperatures below 61º or 62º F., flights occurred only after the rays of sunlight reached the nest. At initial temperatures of 68º F., or more, flights would start as early as 6:15 AM and finish earlier than usual.

Flights took place under both clear and cloudy skies without apparent differences. One flight began under overcast skies and continued for about a minute during a light rain. As the rain increased the flight stopped and the alates sought refuge under leaves, etc. Slight and moderate winds seemed not to affect the flights. No strong winds were noted within the flight season.

A few workers usually preceded the alates from the nest. However, except during the first few flight days at which time the workers controlled the activities of the alates, the workers paid scant attention to them.

Immediately after leaving the nest the alates climbed the nearby leather-leaf branches. On very cool mornings the alates often warmed themselves for several minutes in the sunlight, but on warm mornings there was little hesitation; the alates immediately moved out to high positions on the shrubs. During the first few days of flights the alates were hesitant

about flying. They climbed up and down branches, trying first one and then another leaf tip. Sometimes they would seem to have selected a spot and would start to flutter their wings; then suddenly they would move off to find a more acceptable site. Later in the flight season the alates showed much less hesitation, often flying from the first leaf or terminal stem that they found.

Once the alate had found a satisfactory site from which to fly, it held on with all legs and fluttered the wings, finally releasing its hold and becoming air-borne. The insects usually rose at angles of 45° to 60° from the horizontal until they disappeared over the tree tops 50 to 70 feet above the ground. Sometimes they would circle several times before heading off over the trees. Alates from the nest at Big Cassandra with few exceptions flew toward the north and northwest; those at Mud Lake flew mostly toward the north and northeast. The significance of this orientation to the left of the sun is not known. The only observed deviation from this flight pattern occurred on August 25, 1954 at Big Cassandra when a thick fog lay over the bog obscuring the sunlight. On this day the alates showed no orientation, flying in all directions. In all flights the winged forms flew singly. There was rarely a steady stream of alates in the air such as has been found in some flights of *Lasius* spp. However, on heavy flight days there were often spurts of many alates flying in a few seconds. The flight duration varies from one-half hour to two hours with an average of approximately one hour.

There were no males in the nest at Big Cassandra during the first week of flights in 1954, 1956, and 1957. Apparently in this nest they developed later than the females. At Mud Lake, however, males and females matured in the nest together, and were present throughout the flight season.

Several differences in flight behavior were noted between males and females. When both sexes were present in the same colony, the first alates to come out of the nest in the morning were usually females; males would follow 3 to 10 minutes later. Males, however, were invariably the first alates to fly in the morning. The males flew before the females because they appeared not to be so particular about selecting a take-off point. The nearest stem or branch would do, including some that were only 5 to 8 centimeters above the surface. Females, on the other hand, almost always sought the highest branch or leaf and would often try several to many positions before finally taking flight. When both a male and a female flew at the same time in the same direction, it appeared that the male was a slightly faster flier.

Typically, flights were of moderate size and varied from a few alates at the beginning and end of the season and during the one rainy day to an estimated 300 to 800 per day during late August. On the eighteen days on which flights were observed in 1954 an estimated total of 5000 alates flew. Because a flight season of approximately one month duration is indicated by these records, I believe that 8,000 to 10,000 alate ants flew from each nest within this period.

With so many alates being produced one might expect that colony-founding females and incipient colonies would be found frequently. However, only three colony-founding females were located, and no incipient colonies were seen. One female was found at Hidden Lake on August 11, 1955, in the same hummock as a colony of *D. pustulatus*. A second female was found on August 26, 1955, also at Hidden Lake, on a hummock formed by a dense growth of royal fern. Present in a hollow flowering stalk of a sedge on this hummock was another *pustulatus* colony. On July 28, 1957 the third female was found moving over the moss surface at Big Cassandra. This female was watched for more than a half hour until she was lost in a tangle of leatherleaf. From her behavior she seemed more to be foraging for food than looking for a nesting site. None of the bog nests had developed males or females by this time. Thus, if she was one of a new crop of colony-founding females, she must have developed in some other environment.

DOLICHODERUS PLAGIATUS (Mayr). In the bogs alates were found between August 6 and August 26. A portion of a flight from a single colony was observed at Hidden Lake between 8:00 and 8:10 AM on August 11, 1957. At this time the temperature was 66º F ; the relative humidity was 90 %; the winds were very slight; the sky was clear; and the nest was largely shaded from direct sunlight by the overhanging vegetation. Upon my arrival at the nest site there were three alate females and 25 to 30 workers on the high leaves and stems of a shrub that rose several feet above the nest. It seemed likely that some part of this flight may have taken place prior to my arrival. The alates moved over the shrubbery apparently seeking promonences from which to fly. Prior to becoming air-borne they fluttered their wings several times, and then, releasing their hold on the stem or leaf with the first stroke of the wings, they rose into the air. They flew toward the southeast through an opening in the tree cover. The workers were active on the shrubs while the alates were present, but none of them was seen to come into contact with an alate. Shortly after the last female had flown, the workers returned to the nest.

Colony-founding females of *plagiatus* were found on August 26, 1956 and August 13, 1957 in curled leaves in the leaf-litter of the deciduous hardwood swamp forest near Hidden Lake. Neither of the leaves had been modified to form brood chambers, and the natural openings had not been closed. There was no brood present in either case.

DOLICHODERUS PUSTULATUS Mayr. Alates were found in bog nests between July 15 and August 20. Flights were observed at Big Cassandra on August 9, 15, 16 and 20, 1954, and on August 11 and 13, 1957. The *pustulatus* flights took place from nests located within 12 feet of the described nest of *D. mariæ*, and observations on the two species were made at the same times.

Alates of *pustulatus* flew on mild sunny mornings between 7:15 and 9:30 AM. During these flights the temperatures varied from 63° to 75° F. On mornings with pre-sunrise temperatures of approximately 65° or higher, flights took place before the sunlight reached the nest. On colder mornings the flights were delayed until 15 to 45 minutes after the nest first became exposed to direct sunlight.

After leaving the nest the alates would crawl over the surface and up the branches, stems, and leaves of sedges, cranberries, leatherleaf, and the sporangia of *Polytrichum* moss. Usually, there were a few workers on the vegetation with the alates, but the workers seemed to affect the latter only indirectly. The alates moved over the vegetation, usually settling at the tip of a leaf or stem. Often many such leaves or stems would be examined before they finally prepared to fly. Prior to flying each alate usually held onto the supporting stem or leaf with all legs and fluttered its wings several times. The alate then became air-borne by releasing its hold on the supporting structure on the first beat of the wings. The alates rose into the air at various angles from the horizontal, usually from 45° to 60°, but sometimes almost straight up. No trend was noted in the direction of flight. After an initial climb of 50 to 75 feet the insects rose at lesser angles over the trees and were lost to view. Mating probably takes place in air, although evidence of this is lacking. There was no indication that mating ever takes place in the nests.

The *pustulatus* flights seen never included more than 20 to 30 alates per nest on a flight day and usually fewer. Flights of *pustulatus* are, therefore, of the sparse type.

Colony-founding females have been found in late summer and fall in curled leaves and hollow stems. Each of the stems and leaves examined was found to have some naturally occurring opening through which the female could enter or leave the cavity. For this reason it is believed that the female forages for food while her first brood develops. Although the female may select her brood chamber in the summer, she does not lay any eggs until the following spring, and the first workers do not mature until mid-summer.

CAMPONOTUS NEARCTICUS Emery. Alates were found in nests as early as August 19, and were present throughout the winter months. Flights probably take place in late spring or early summer, but none were observed. The newly mated females seem always to seek cavities in which to start new colonies. Apparently, colonies will remain in the same nest site or occupy additional similar nest sites after the colony has reached maturity. Thus, colonies that occur in decaying logs or stumps probably originated in a cavity in the log or stump, while colonies that originated in hollow stems probably expand into segments occupying several, not necessarily contiguous, stems.

CAMPONOTUS NOVEBORACENSIS (Fitch). Gaige (1914, p. 29) recorded alates in nests on the Charity Islands, Michigan on September 22,

1910, and Headley (1943a, p. 29) found them on July 30, 1938 in a nest in northeastern Ohio. In the bogs males and females were found in nests between August 16 and June 7. Their nuptial flights probably occur in late May and June, although none were seen. A possible prelude to a flight was observed on June 7, 1956, in the larch swamp at Hidden Lake. Workers from a colony nesting in a log lying on the surface were very active about the nest openings and on the log and nearby vegetation. No alates appeared outside the nest during the time of observation, from 2:00 to 3:20 PM. Because it was impossible to remain longer, the nest was opened. Many alates were found at or near the entrance, so that it seems probable that a flight might have occurred later that afternoon.

Colony-founding females were frequently found in wooded areas in small chambers under loose bark and in pre-formed cavities in wood. One small colony found in the marsh area near Hidden Lake was of interest because it was in a nest formed of a large round chamber (about 8 centimeters in diameter) in a tussock of sedge and grass roots. Wood was virtually absent in the vicinity of this nest, and this may have been the reason for the unusual nest site. All mature colonies were found in wood.

The sequence in brood development during the colony-founding process seems to be as follows: 1) female finds a small cavity in late May or June and occupies it, probably modifying it to make it the right shape and size; 2) the chamber is sealed shut from the inside; 3) the first eggs are laid and the first larvæ hatch in June and early July; 4) the larvæ grow during July with pupæ forming late in July and in early August; 5) additional eggs are laid in early August; these develop into larvæ before the onset of hibernating conditions; 6) the first workers mature during mid—or late August and the colony is established.

LASIUS ALIENUS (Foerster). Wilson (1955, p. 86) stated that in North America most alates occur in nests in August. Although no flights were seen in the bogs, they likely occur in the middle or late afternoon during late July and August, and are probably "spectacular." It is apparently unusual for bog colonies of this species to make external nest modifications during the flight season. Of more than a dozen nests examined in the bogs in late July and early August of 1956, only one had been modified. In this instance a chamber 3 centimeters high was formed on the top of a log from debris brought from the inside of the log nest. Alates and workers were present in this chamber at noon of August 7, 1956.

The brood chamber of a newly formed nest, which is usually 2 to 3 centimeters long by 1½ centimeters wide, has its inner surface always rather smooth and clean. Its entrance is completely closed by a wad of debris (probably some of the material removed in the making of the brood chamber) until the first workers mature. The finding of a number of dealate females in chambers near a mature colony suggests that some

mating may have taken place in the nest, following which the females may have crawled out of the nest to establish colonies in nearby sites. Several females were found sealed in separate cavities on August 7, 1956, with only eggs in the chambers. These females had presumably mated a week or two before they were located, and had just laid their first eggs. A female collected on August 29, 1956 had several tiny larvæ with her in the chamber. However, a colony-founding female collected on April 6, 1956, had no brood whatsoever, suggesting that some females overwinter without producing any brood. Perhaps this is the result of a difference in mating times in that the females which start their colonies late in the fall do not lay eggs until the following spring. On the other hand, it is also possible that the female may have eaten the eggs and larvæ that were present the previous fall.

LASIUS MINUTUS Emery. Gaige (1914, pp. 21-23) recorded alates in nests between September 17 and 20, 1910, at the Charity Islands, Michigan. Wilson (1955, p. 182) cited alates from nests in August and September in Massachusetts and Ohio. In the bogs alates begin to appear in the nests as early as July 30, males usually developing before the females. However, flights apparently do not occur for several weeks after the first alates have matured. Flight activities were observed at a single nest in the larch-sphagnum community at Mud Lake Bog in 1954 and from eight nests in the larch swamp near Hidden Lake in 1956. The first flight in 1954 appears to have taken place on August 18; in 1956 no flights occurred until August 25. In the latter year alates flew from various nests (but not all) on six additional days until September 9, when observations ceased. At this time there were still alates present in nests, indicating that the flight season was not over.

Throughout most of the year *minutus* mounds are characterized by even surfaces without external openings. A few days prior to the first flight, the workers would begin to form tunnels just beneath the surface of the mounds with a few openings to the surface. Gradually these openings would become enlarged during the flight season by the removal of the roofs of the tunnels until the nest surfaces ultimately took on a finely-ridged appearance.

On a flight day pre-flight activity began about 1:15 to 2:00 PM, at which time workers would appear in the openings. In those portions of the nest which were shaded, the workers would soon come out onto the surface. The alates, however, were held back by additional workers at the entrances. Both workers and alates remained in the nests in those portions that were in direct sunlight. Workers were found to appear on the surface and alates to gather in the openings prior to flight at temperatures varying from 67° to 85° F. Alates were seen to fly at temperatures between 70° and 84° F.

A major climatic influence on the flight activities of *minutus* was sunlight. Generally, neither workers nor alates would appear on the

surface in the direct sunlight. Flights normally occurred between 2:00 and 5:30 PM when the nests were shaded. Nests which were situated in open areas had flights at normal times on cloudy days, but on clear days had flights only when shaded from the sun during late afternoon. Nests which were shaded by vegetation from the south and southwest sunlight had flights at about the same time on clear days as on cloudy days, i.e., early to mid-afternoon. Nests in open areas on partly cloudy days might have considerable activity on the surface or even flights when clouds obscured the sunlight, but when the clouds passed and direct sunlight again reached the nests, all above-surface activity ceased, with the alates and workers immediately returning to the nest.

Examination of the barometric pressure records obtained at the George Reserve during the flight season of *Lasius minutus* (and also *Lasius speculiventris*) in 1956 showed that the pressure was falling very gradually each day during the flight period. The pressure varied between 29.60 and 30:00 inches at the times of flights. Similar conditions prevailed, however, on days when flights did not take place. There were no major pressure changes immediately before or after the flight season. Hence, the evidence that flight activities are influenced directly by barometric pressure is inconclusive.

Eight *minutus* mounds were observed daily in the afternoon from early August until September 9 in 1956. On the basis of these observations it was determined that the environmental conditions under which flights took place were similar for these nests, but on a given day with the same or similar climatic conditions in the area some nests had flights while others did not. Thus, flights do not occur just because the conditions are proper. When conditions are proper, flights *may* take place. The absence of flights from all nests on the same day suggests some means of control from within the colony.

Alates of *minutus* would fly from any projection, utilizing sedge stems, branches of adjacent shrubs and trees, and the moss, cranberries, and soil on the surface of the nest. Because of their abundance on the nests, sedges were most frequently utilized. As a rule, the first flight of the year from a nest was almost exclusively a male flight; females usually did not fly until the second flight day. Males greatly outnumbered the females during all flights. It was estimated that between 5,000 and 30,000 alates flew on days of heavy flights. On the most favorable days the flight might last as long as one and one-half to two hours. Most of the flights that were observed were sporadic because of the influence of direct sunlight, and therefore lasted only a few minutes at a time.

During the height of a flight there was no hesitation about flying; the alates reached the ends of projections and immediately flew. At other times the alates seemed to "jockey for position" by trying first one and then another projection. At the instant preceding flight each alate held on to a stem or other object with all legs; on the first stroke of the wings it released its hold and rose virtually straight up into the air. There was

no fluttering prior to flight. The alates usually flew towards light, open regions between forested areas, but seldom directly towards or away from the sun. The alates rose up at angles of 60° to 80° from the horizontal to a level above the trees, gradually leveling off before being lost to view. No large "clouds" of alates were formed from these nests, although at the peak of a flight a steady black stream of ants rose into the sky. Apparently, *minutus* alates do not form swarms, for none were seen. The alates probably mate principally in the air; but some mating may take place in the nest, for shed wings have found in nests on several occasions.

Colony-founding by *minutus* has been presumed to be parasitic (Creighton, 1950, p. 421; Tanquary, 1911, pp. 300-302; Wilson, 1955, p. 182), but no evidence of mixed colonies was found in the bogs. Although thousands of alates were known to fly from individual nests, only a few colony-founding females were found. All of these were in small chambers in the loose soil just beneath the surfaces of mounds that were already occupied by flourishing colonies of *minutus*. It is possible that these females had mated within the particular mounds and then merely moved out to the surface of the mound, or that they took part in a flight, dropped to the ground, found a mound, and buried themselves in the soil, thus acquiring the nest odor. The matter, of colony-founding by the bog species of *Lasius* is discussed in a later section.

LASIUS SPECULIVENTRIS. Emery Wilson (1955, pp. 172-173) cited collections of *speculiventris* alates made in August and September in Michigan and Minnesota, and a single alate female taken in Kansas in June. In the bog nests, alates have been found from August 2 to September 9.

Three colonies of this ant, which were located in the Hidden Lake area near the eight nests of *minutus* mentioned above, were observed daily in 1956 from early August until September 9. Flights took place daily between August 27 and 30. No further flights were seen after the latter date; however, alates still remained in the nests until September 9 when observations ceased. Additional flights probably took place later.

Typically, flight days of *speculiventris* were warm, humid, calm, and cloudy. Although the workers and alates became active in the nest entrances as early as 1:15 PM, flights did not occur until later. Flights began as early as 2:35 PM and as late as 4:20 PM; flights terminated as early as 2:45 PM and as late as 5:15 PM. Temperatures recorded during flights varied from 77° to 85° F. Flights occurred early in the afternoon at the higher temperatures, but with lower temperatures the flights took place in late afternoon. A very important environmental feature that affected flights was shading of the nest area. Flights occurred on clear days only when the nest area was shaded by vegetation. Because the nests at which flights occurred had south and west exposures, flights on clear days took place in late afternoon. The alates flew earlier in the

afternoon on cloudy days. On partly cloudy days flights began early if the nest were shaded, but ceased with the alates and workers returning to the nest if the nest area was again exposed to direct sunlight. Soon after the nest area was shaded again, the alates and workers returned to the surface and vegetation.

Several days prior to the first flight the workers prepared the nest surface for flights. Many openings were formed on the nest surface, and these were gradually enlarged during the flight season. Before every flight several hundred workers preceded the alates from the nests. Most of these workers acted as guards at the entrances, apparently keeping the alates within the nest until conditions were suitable for flights. A few, however, moved out onto the surface and vegetation as if to see that the conditions were right and that nothing would hinder the flight. The workers at the nest entrances gradually gave ground to the surging mass of alates within the nest by moving out of the entrances onto the surface and vegetation. The alates, once out of the nest, did not spread out over the surface and vegetation, but followed the workers and stayed in line behind them. Thus, these lines of alates headed by a relatively few workers slowly advanced up the vegetation, the alates forcing forward, the workers doing their best to hold them back. Under suitable climatic conditions, it would take 20 to 30 minutes for the alates to reach the tops of the vegetation, at which time they were able to break through the worker guards. From this time until the flight was over and all had returned to the nest, workers continually circulated among the alates apparently stimulating them to fly. Toward the end of the flight the workers would begin stimulating the alates to return to the nest.

The alates usually flew from projections such as leaves and stems of grasses, sedges, and shrubs, and from stumps and logs. However, during heavy flights they often flew directly from the nest surface. Early in a flight there was often much hesitation about flying, and considerable movement over the vegetation, etc. When a flight was at its peak, the alates did not hesitate, but flew immediately. There was no fluttering prior to flight, the alates releasing their hold on the projections at the first stroke of the wings. They rose upward at 60° to 80° toward open areas, but rarely towards the sun. Males seemed always to be more numerous than females, usually greatly in excess. The first flight observed was almost exclusively a male flight. On that day only 50 to 100 alate females emerged from the nest, and not all of these flew. In each of the other flights the females were out by the thousands, but apparently never outnumbered the males. Flights of *speculiventris* are of the mass type, with many thousands flying per day. An average of several hundred alates flew per minute with occasional spurts of several thousand per minute. Although workers and alates might be active outside the nest for three hours or more, the flights seldom lasted for more than an hour to an hour and a half. Sometimes flights were interrupted because of the effect of direct sunlight on the nest.

Mating appears to take place in the air, on the nest surface, and in the nest. One of the colonies observed gave evidence that all of the alates took part in the nuptial flights, and therefore all mating presumably took place in the air. Another colony was observed to have large flights and also to have mating take place on the nest surface between several hundred known members of the same colony. In addition, some mating was presumed to have taken place within the nest. Intranidal mating was indicated by finding several hundred dealate and partially dealate females emerging from the nest on two afternoons, and by finding shed wings in the nest chambers when the nest was opened several days later.

If *Lasius minutus* is a social parasite, then *Lasius speculiventris* is a social hyperparasite. Some mature nests of *speculiventris* contained a number of *minutus* workers; other nests appeared to be purely *speculiventris*, as they would be expected eventually to become, since these are not true slave makers. The type of nest structure is similar to that of *minutus*, and the areas of occurrence are common to the two species. Because *speculiventris* is much the rarer of the two ants, and because most of the mixed colonies that were examined produced only alates of *speculiventris*[5], this latter ant must be parasitic in its colony-establishing behavior. It is possible that small colonies or outposts of *minutus* nests are used for the beginning of a new colony. However, judging from the size of several mixed colonies and the very large number of *minutus* workers present, it is also possible that larger colonies are attacked.

Colony-founding was observed on August 28 and 29, 1956. A group of *minutus* mounds that were several hundred feet away from the nearest *speculiventris* colony were being invaded by several dealate females of *speculiventris*. How these females reached these mounds was not observed, but it is believed that they dropped on the surface nearby after a flight, cast off their wings, and then invaded the nearest mound. On the mound surfaces several of these females attempted to form chambers in the top layer of the loose soil and seal themselves in. One female was dug out of such a subsurface chamber. It is likely that this procedure permits the female to acquire the nest odor so that later she would be able to enter the nest galleries without being attacked by the workers.

Other females were more bold and attempted to enter the nest through the entrances (which, because it was also the flight season for *minutus*, were present on the surfaces). Workers were present in the entrances or the galleries just below them, and immediately began to attack the intruding females. The females when attacked appeared to feign death and allowed themselves to be moved about on the nest surface. If discarded by the *minutus* workers, the *speculiventris* females would once again attempt to enter the nest. Although the *minutus* workers bit the *speculiventris* females wherever possible and as long and often as possible, in no instance were the latter seen to be provoked into retaliating on the former. Ulti-

(5) One mixed colony of *minutus* and *speculiventris* produced males and females of both species. These alates all flew at the same time.

mately several of these females were seen to be carried into the nests. Other less fortunate females ceased in the efforts to penetrate the nests, and retired to the cover of the nearby vegetation in early evening. They were never seen again.

A very unusual case of parasitic behavior was noted on August 28. On this afternoon alates of *speculiventris* were leaving a mixed nest of *speculiventris* and *minutus*. Some of these flew off; others mated on the nest surface and immediately cast off their wings. Still other females were emerging from the mound in dealate condition implying that had been fertilized in the nest. Some of the dealate females in these last two groups promptly began attempting to form chambers not only in the nearby *minutus* mounds, but also in the same mound in which they had developed.

LASIUS UMBRATUS (Nylander). No flights of this ant were observed in the bogs. A single alate female found alive (1:30 PM) in a spider's web in the deciduous hardwood swamp at Mud Lake on September 26, 1954 indicates that a flight occurred during the early afternoon on that day. Wilson (1955, p. 163) states that in North America alates are present in nests of this ant from late June to late October, without indicating whether or not regional differences occur. Records from southeastern Michigan (University of Michigan Museum of Zoology) indicate that in this region most alates occur in nests from mid-July to early October.

Although *umbratus* is supposed to be parasitic in its colony-establishing behavior, no evidence of this type of behavior was observed in the study areas. Dealate females without brood were frequently found in closed soil chambers under moss at the bases of trees in the deciduous hardwood swamps at both Mud Lake and the George Reserve in May of 1953 and 1956. Despite intensive search no incipient colonies could be located later in the summer.

FORMICA FUSCA Linnaeus. Alates were found in nests between July 6 and August 13, but were rarely abundant. Flights appear to be inconspicuous as attested by the fact that only a single flight was seen during this study although daily trips were made to the bogs at times when flights probably occurred.

A flight of males from one of the colonies in the leatherleaf community on Big Cassandra Bog was observed on August 2, 1956. The flight was in progress at 8:40 AM and continued until 9:30 AM. During this period the temperature increased from 69° to 75° F. I do not know how many alates flew prior to 8:40, and whether there were any females among them. Most of the *fusca* colonies examined during the flight season contained only one sexual form, or had one sex in great predominance. No females were found in this particular nest in 1956. During the 50 minutes of flight about 20 to 25 males flew. There were few males on the shrubbery

and nest surface during the flight.   Instead they kept coming out of the entrances throughout the flight period.   At the end of the flight the workers chased the remaining males back into the nest.   All the males flew from the shrubbery surrounding the nest.   They crawled over the branches rather quickly, but uncertainly, and usually for only a minute or two before selecting a site from which to fly.   Once in the the air the males rose upward at 60° to 80° angles, flying high over the adjacent upland forest trees and disappearing from view.

Only a single colony-founding female of *fusca* was found in the bogs. She had formed a small chamber (18 millimeters long by 10 millimeters high by 15 millimeters wide) about three centimeters below the soil surface in the larch swamp near Hidden Lake.   The chamber, which was sealed shut from the inside, contained several small larvae when discovered on August 7, 1957.

FORMICA NEORUFIBARBIS Emery.   Pupae of the sexual forms were found in nests from July 8 to August 3, but alates were seen only on August 2 and 3.   No flights were observed.   It is suspected that the alates fly within a few days of emergence from the pupal case.   Flights, therefore, probably take place from a particular nest on several to many days scattered over a period of a month or more.   On the morning of August 3, 1954, a callow alate female was found in a nest.   This female and a number of workers and pupae were taken to the laboratory and kept in an artificial nest.   By the evening of August 3, three females had emerged from the pupal cases.   They were light yellowish in color and had fully expanded wings when observed.   On the morning of the 4th, females had emerged from all of the remaining pupae.   These alates began to take on color gradually.   By the 7th they were still not fully colored but were attempting to fly.   The female which had been found in the nest had shed her wings on August 5th.   She could not have mated because there were no males produced in that nest during the year. Probably, this reaction was brought on by her imprisonment in the artificial nest.

In nature, colonies were established independently in small chambers formed by the females in the peat, moss, or debris on the surface.   The chambers were about 2 centimeters in diameter, round and rather smooth surfaced.   They were built in the top 8 centimeters of the moss and peat. Each chamber had a single which was closed by packed soil.   No brood was present in any of these chambers in late July, indicating that the females had just formed the chambers.   Probably eggs are laid in August and these hatch into larvae before the onset of winter.

FORMICA ULKEI Emery.   Holmquist (1928, pp. 77-78) found alates in nests between July 14 and 23 in the Chicago region.   Because no mature colonies were found in the bogs, no information is available on flights in this environment.   An incipient colony of *ulkei* was found in a small

mound at Hidden Lake; *Formica fusca* was the host.   A ratio of host workers to parasite workers of 20:1 was evident in a total population of approximately 1000 workers.

FLIGHT COMPARISONS

MYRMICA spp.   Reasonably complete accounts of flights of three species of *Myrmica* in east-central United States are now available: *M. americana* in southeastern Michigan and northwestern Ohio (Kannowski and Kannowski, 1957), *M. emeryana* in north-central Ohio (Talbot, 1945), and *M. fracticornis* in southeastern Michigan bogs.   *Myrmica* alates are present in nests in summer and early fall, and flights take place during this same time.   However, in this same area each of these species has a distinct flight season.   The time of year that the flight season occurs is relatively constant for each species, variations resulting from seasonal climatic differences and microenvironmental conditions.

The flight periods of these three species are quite distinct.   Talbot (1945) found that *emeryana* flew mostly between 6:00 and 8:00 AM, while *americana* flights were found to occur mainly between 12:30 and 4:30 PM (Kannowski and Kannowski, 1957).   From the observations recorded above, it is evident that *fracticornis* flies usually between 6:00 and 7:30 PM. However, it is interesting to note that Talbot found a few alates of *emeryana* flying in late afternoon, while I found some *fracticornis* alates flying in early morning.   This unusual situation is evidently the result of similar climatic conditions at these times.

A survey of the climatic conditions under which flights take place indicates considerable latitude in temperature response for all three species, but most especially in *americana*.   This latter species was observed to have flights at temperatures varying from 64° to 88° F.   All three species have flights mainly at times of reduced light intensities: *fracticornis* in early evening, *emeryana* in early morning, and *americana* usually under shaded conditions.

Flights of these three species are usually of the sparse type, and I suspect that this holds true for most species of *Myrmica*.   Discontinuous flights are usual for *americana*, *emeryana*, and *fracticornis*, and probably also for most of the remaining species in this genus.   No swarms were noted in these three species, but Eidmann (1933, p. 203) recorded swarming of *fracticornis* on August 11 and 29, 1931 in Quebec.   Swarming has also been observed of other species of *Myrmica* (see Chapman, 1954, 1957; Donisthorpe, 1927, pp. 115-116; McCook, 1879, p. 142; Neubecker, 1952; Reaumur, 1743, pp. 165-167; Samsinak, 1950; and Weber, 1935, p. 167). Two excellent photographs of *Myrmica scabrinodis* swarms are presented by Neubecker (1952).

Copulation by *americana* alates was observed to take place both in air and on the ground (Kannowski and Kannowski, 1957, p. 373), and this

has also been observed for other species of *Myrmica* by Reaumur (1743, pp. 165-167), Crawley, and Bond (Donisthorpe, 1927, p. 115). Females of *americana* were seen to copulate with males presumably of the same colony. Intranidal mating, which was presumed to take place in bog nests of *fracticornis*, evidently also occurs in *americana* nests (Kannowski and Kannowski, 1957, p. 374). Some, if not most, of the polygynous *Myrmica* colonies probably result from intranidal mating with one or several of these females remaining in the nest.

DOLICHODERUS spp. Flights of *Dolichoderus mariae* alates have now been observed from an upland field nest (Talbot, 1956) and from a bog nest (see above) at the same locality (E. S. George Reserve, Michigan). Comparison of the flights from these two nests shows a few differences which may be the result of the environmental variations, and some similarities which may be considered as characteristic behavior of this species.

The nest studied by Talbot was on the side of a northwest facing slope and, thus, did not benefit from the warming effect of direct sunlight as the bog colony did. This accounts for the differences in temperatures at which the females flew in the two habitats. Females flew from the bog colony at temperatures as low as 56º F., while at the upland colony they were observed to fly only at temperatures of 63º F. or higher (Talbot, 1956, Table 1). The maximum temperatures at which flights occurred were slightly higher in the bogs (78º F.) than on the upland hillside (74º F.).

These observations indicate that the flight season, flight period, and flight duration are similar for the two colonies in the same locality with only slight differences due to the environment. The flight season begins in early or mid-August and lasts until mid-September. The flight period extends from 5:28 AM to 10:45 AM. The flight duration apparently averages about one hour but varies considerably with the temperature. The flight duration on cool mornings (approximately 65º F. or less) is much longer than on warm mornings (more than 65º F.). Flights are continuous, except during inclement weather, and are of moderate size.

Certain aspects of the behavior of the alates were alike or similar at the two colonies. The alates climb the adjacent vegetation to gain prominences from which to fly. Before flight, they spend considerable time moving over the vegetation trying first one and then another site before settling on one. This behavior is most noticeable on cool days. The time consumed from the time of emergence from the nest to the time of flight is generally much less for males than for females. The males are much less hesitant about flying, often leaving from the first projection found. After a daily flight, the alates which did not fly move down from the vegetation and return to the nest. Workers often assist in this project. Some of the alates then parade on the nest surface.

Flights have not been reported for the closely related species, *D. tas-*

chenbergi (Mayr) (6). However, Logier's observation (1923) of alates parading on the nest surface in mid-morning indicates that many of the flight activities of these two species are probably quite similar.

Much less is known of the flight activities of *D. plagiatus* and *D. pustulatus*. It is certain that the flights of these two species take place at the same general time of the year as *mariæ*. They also occur in the early morning and under similar temperature conditions. The alates of *pustulatus* evidently respond to temperature in a manner similar to *mariae*, and it is probable that *plagiatus* alates do likewise. Flights of *pustulatus* and *plagiatus* are of sparse size, due mainly to the small colony populations of these two species. Like *mariae*, the alates of *plagiatus* and *pustulatus* fly from the nearby vegetation. Flights take place from prominences, usually the ends of leaves or stems. The alates of these three species may flutter their wings prior to flight. After a daily flight, the alates which did not fly return to the nests, usually as the result of worker stimulation. Unlike the alates of *mariae*, those of *pustulatus* do not come back out of the nests until the next flight day.

LASIUS spp. Because colonies of *Lasius* are usually common in north temperate regions, and because the flights are usually conspicuous, probably more flights of *Lasius* species have been observed by myrmecologists than of species of any other genus. Few of these flights, however, have been adequately described. The flights of "*Lasius niger alienus americanus* Emery" [*L. neoniger* (Emery), det. E. O. Wilson] described by Talbot (1945, pp. 504-506) are the only ones for a North American species of this genus which have been sufficiently studied and therefore provide a comparison for the two species studied in the bogs. I have also included unpublished data on the flights of *Lasius neoniger* Emery, which I have observed from crater nests in the Ann Arbor, Michigan, vicinity.

Lasius flights usually occur between mid-summer and mid-fall, and almost always take place between early afternoon and early evening (Donisthorpe, summarization of European work, 1927; Eidmann, 1926, 1933; Forbes, 1908; Forsslund, 1949; Gaige, 1914; Gösswald, 1938 ; Kutter, 1946; McCook, 1879; Rau, 1934; Reaumur, 1743; Talbot, 1945, and in Wilson, 1955, p. 136; Tanquary, 1913; and Turner, 1915). However, Rau (1934, pp. 207-208) recorded a most unusual flight from two *Lasius umbratus* colonies which occurred between 6:30 and 7:45 AM at St. Louis, Missouri. Mass flights are common for *minutus* and *speculiventris*, and may sometimes occur in *neoniger*. *Lasius neoniger* flights from a single nest entrance may be of only moderate size. For the last three of these species the initial flight of the season may be very small and sporadic.

Lasius alates respond distinctly to various climatic conditions. Moderate temperatures prevail during most flights, but probably there is some

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(6) Flights of *D. taschenbergi*, a species which has not been found in bogs in southeastern Michigan, were observed from an upland community on the George Reserve in 1957 and will be described in a future paper.

variation of temperature response by alates with the season of the year. Flights usually commence after the warmest part of the day has been reached and proceed as the temperature slowly decreases. They do not occur on hot days (above approximately 85° F.), perhaps because of other climatic conditions in addition to excessive temperatures. Flights take place when relative humidities are moderate to high, but are absent when low. This factor may not have been critical in the bogs where moderately high humidities generally prevailed at the nest level. Flights which commence in early or mid-afternoon occur during rather high light intensities, but during most flights, the intensity is gradually decreasing. *Lasius neoniger* alates seem to adjust to considerable variation from high intensities of mid-afternoon to the dim light of early evening. In addition to an adaptation to decreasing illumination, *Lasius brunneus* (Forsslund, 1949, p. 21) and some other species in this genus show definite negative responses to direct sunlight. In the case of both *minutus* and *speculiventris*, flights would stop, and the alates and workers would return to the nest chambers if direct sunlight reached the nest. Because of topographic and vegetational features of the environment, colonies situated only 50 feet apart, may have flight times at different hours. Turner (1915), however recorded a flight of "*L. niger*" (misdetermination;=*L. neoniger*?) that began in full sunlight, and I have also observed this occasionally for *neoniger* flights in south-eastern Michigan. The occurrence of flights immediately before or after rains (Rau, 1934, p. 209; and Talbot, 1945, p. 506) suggests that atmospheric pressure may affect flights. However, positive correlation of flights with atmospheric pressure changes has not yet been shown. A thorough study of this association would be desirable.

A few days prior to the beginning of the flight season, the workers from *Lasius* colonies begin to prepare entrances for the emergence of alates. For the epigeic species, of which the crater-forming species, *neoniger*, and also *alienus* are examples, nest entrances are open throughout the summer months. Prior to flights the workers enlarge these entrances and some-times make new ones. *Lasius minutus* and *speculiventris* are examples of hypogeic species, and their mounds are normally without external openings except during the flight season and when the nests are repaired or enlarged. Thus, the formation of entrances on the nest surface is the first indication of an approaching flight season.

Soon after the entrances have been prepared, alates and workers are found clustered in the passageways below the openings in the afternoons. Evidently the workers restrain the alates until times of proper environmental condi-tions. The first flight is usually a small one. For *neoniger*, as well as the two bog species, the first flights are almost exclusively male ones; females do not become abundant until the second or third flight days. Thus, the female population is conserved until the flight season is well established and a large breeding population is assured. Males evidently greatly outnumber females, therefore making the chances of successful fertilization high.

FORMICA spp. Flights have been described for *Formica pallidefulva nitidiventris* Emery and it's synonym "*F. pallidefulva schaufussi incerta* Wheeler" (Talbot, 1945, 1948), *F. subintegra* (Talbot and Kennedy, 1940) and *F. obscuripes* (Weber, 1935). In addition to the bog flight, I have observed two flights from *Formica fusca* colonies in lawns at Ann Arbor and Howell, Michigan, in July of 1955 and 1956 respectively. The flight season for the Formicas extends from late spring to mid-summer. *Formica* flights apparently always take place in the morning hours (Burrill, 1910, p. 127; Talbot, 1945, 1948; Talbot and Kennedy, 1940; Wellenstein, 1928, p. 7), but with considerable variation as a result of climatic conditions. Thus, the *fusca* flight at Ann Arbor took place between 7:00 and 7:45 AM on a warm morning (72-75° F.), while the flight of the same species at Howell was seen at 11:30 AM because of cooler temperature (69° F.).

A peculiarity of *Formica* is the occurrence of flights consisting exclusively or almost entirely of one sex. This happens because colonies tend to produce either males or females exclusively, or else one sex in great predominance. However, as Forsslund (1949, p. 24) has stated, we have information on too few species to know if this is a characteristic of most Formicas. With the exception of very populous and/or parasitic colonies, such as those of *subintegra* (Talbot and Kennedy, 1940), flights are usually composed of rather few individuals (usually less than 50 and often less than 25). In these sparse flights the individuals emerge singly over a period of an hour or more and rather quickly fly. A flight duration of approximately one hour means that few alates are seen outside the nest at a time. As Talbot (1945, p. 509) has so aptly described it, "casual observation even during what might be called the peak of flight might reveal nothing."

The nests of *nitidiventris* (Talbot, 1945, p. 509) and of *fusca* are not appreciably modified during the flight season. The number and size of the entrances remain about the same, so that there is no external indication of the occurrence of flights. During a flight the alates leave the nest and rapidly move onto the nearby vegetation. There they find prominences and fly almost immediately. Fluttering prior to flight is rare, but has been observed by Weber (1935, p. 189) for *obscuripes*. The workers take little or no part in the flights of *nitidiventris* (Talbot, 1945, 1948), *obscuripes* (Weber, 1935), and *fusca*, but Talbot and Kennedy (1940) indicate some worker activity in terminating flights of *subintegra*.

DISCUSSION

Flight Activities.

1. *Number of flights.* The flights of some species of ants are spectacular and the cause of no few short notes on "the mating flight." Wheeler (1910, p. 183) stated that "the nuptial flight for all the colonies of a

particular species in the same neighborhood usually takes place on the same day or even at the same hour." This fallacy has prospered to the present among prominent myrmecologists even though abundant evidence has accumulated to negate Wheeler's view (see Talbot, 1945, p. 504).

On the basis of the observations recorded above, it is certain that flights of all the species observed take place on more than one day, and may even occur over a period of several weeks. In those species whose flights were not observed, a long flight period is indicated for most by the presence of alates in nests during a two to four week period, and by the finding of recently dealated females attempting to establish colonies during the time that alates are still present in nests.

2. *Concurrent flights.* Wheeler's statement that all the colonies of a species in a given area have flights on the same day appears to be the exception and not the rule. Only *Dolichoderus mariae* seems to fit this category, for flights occurred from a nest in an upland community (Talbot, 1956) and from bog nests on the same days. Most of the species of bog ants did not have daily flights, and even in the case of one (*Tapinoma sessile*) that was quite regular, not all colonies had flights each day.

3. *Daily flight time.* Flights from different colonies of a species in a locality usually take place at about the same time with only slight variation due to microclimatic differences. This is shown by comparison of the flight activities of *Dolichoderus mariae* from a bog colony with those of the upland colony observed by Talbot (1956). In addition, observation of *Lasius minutus* and *Lasius speculiventris* colonies in the bogs showed distinct variations in daily flight time which were correlated with environmental conditions in the vicinity of the nests.

The time of the day that flights occur is often similar for closely related species. The flights of all three species of *Dolichoderus* in the bogs took place in early morning, and all flights of *Lasius* were seen in the afternoon. *Formica* flights evidently always occur in the morning hours. Some variations due to environmental differences are evident, but there appear to be basic innate patterns in these genera responsible for maintaining these flight times. In *Mymica*, on the other hand, the flight time differs markedly among the species in this region. It seems possible that the similarity of flight times among species in a genus often results from rather recent speciation in the group. This would account for *Dolichoderus*, *Formica*, and *Lasius*, which are evidently recently evolved taxa. *Myrmica*, however, is a rather primitive myrmicine genus and shows greater behavioral variation. This might be the result of greater divergence of the particular species.

4. *Yearly flight time.* The time of the year that alates mature appears to be similar for closely related species and is probably due to similar innate behavior patterns. The alates of the three species of *Dolichoderus* in bogs mature at about the same time, because in each case they develop from eggs laid at about the same time (late May and June). That the alates of one of these species mature a few days or weeks prior to those

of the others is explainable on the basis of environmental factors which bring about more rapid development of the brood. The colonies in those microhabitats which are warmest and driest will bring forth alates before the colonies in the more moist and shaded sites do. However, Headley (1943b) found two species of *Leptothorax* occupying identical microhabitats under seemingly identical conditions, but one species became active and began egg-laying almost one month earlier than the other. This month's difference in activity appears to account entirely for the difference in the time of alate maturation. Physiological tolerances may, therefore, affect the time of the flight season.

It is interesting that the flights of *Myrmica brevinodis*, a species that was found nesting only in the permanently moist parts of the bogs, occur at the time of the year the bogs are driest. Therefore, the alates reaching moist environments would likely be more successful in colony establishment. The absence of colonies in the drier parts of the bogs suggests that alates do not come to these areas or are unable to survive there.

5. *Flight size.* Flights of various sizes were observed in the bogs. The size of a flight depends upon the size of the colony, the regularity of flights, and the length of the flight season. Species whose total population is probably no more than one to two thousand individuals per colony have sparse flights, while species with populations of many thousands of individuals per colony may have mass flights. However, if the alates fly as soon as they mature (as exemplified by *Dolichoderus mariae* and *Formica fusca*), flights may be sparse to moderate even if the colony populations are very large. Species whose alates remain in the nest until all have fully matured (such as *Lasius minutus* and *Lasius speculiventris*) are likely to have a few spectacular mass flights.

6. *Site of mating.* Mating may take place in the air, on the surfaces, or in the nest. Aerial copulation may result from the union of randomly dispersed alates or from the union of males and females from a swarm of alates. The chances of mating in the air taking place are slight under conditions of solitary flight, good under mass flight conditions, and best in the case of swarming. Intranidal mating (7) may occur prior to flights. However, among the bog species, females which had mated in the nest usually seemed to divest themselves of their wings immediately, a condition possibly brought about by the process of copulation. So far as is known, alates of none of the bog species mate only in the nests. Therefore, intranidal mating is an exceptional process, not a normal one. Its cause is unknown. In populous colonies, such as *Lasius* spp., retention of the alates in the nests for several weeks after they have matured may possibly bring about a breakdown of social organization resulting in intranidal mating.

The type of mating behavior is important in determining the ecologic, as well as the geographic distribution. Intranidal mating, if not followed

(7) Proof of intranidal mating may be obtained by examining the seminal receptacle in the female for living sperm.

by a flight, may result in decreased dispersion, and may maintain a maximum population density in a restricted area. On the other hand, mating methods which include flights promote the dispersion of the species.

Colony=Founding.

1. **Social parasitism.** — *LEPTOTHORAX DULOTICUS* Wesson. Nothing is known of the natural colony-founding behavior of *Leptothorax duloticus*, although Wesson (1940, pp. 79-80) observed the behavior of females in captive colonies of *Leptothorax curvispinosus*. However, he failed to get any positive results. According to Talbot (1957), the usual slave in upland communities in southeastern Michigan is *curvispinosus*. In the bog habitat *curvispinosus* is rare, while *Leptothorax ambiguus* is quite common in certain communities. If a *duloticus* female is going to establish a colony within a bog, its chances of success are poor for several reasons. First, of the four species of *Leptothorax* available to enslave, only *ambiguus* is abundant. The two species which are frequently recorded as slaves, *curvispinosus* and *longispinosus* by Wesson (1940) and Talbot (1957), are the least common in bogs. The fourth species, *muscorum*, has never been known to be enslaved by *duloticus*, although it has been recorded by Smith (1939, 1951) and Gregg (1945) as a slave of *Harpagoxenus canadensis* Smith in eastern Canada and northeastern United States.

The present collection is the first record of enslavement of an *ambiguus* colony. Talbot (1957) subsequently found several *ambiguus* workers in each of seven mixed colonies of *duloticus* and *curvispinosus*.

The rarity of *duloticus* in nests of *ambiguus* and its absence in nests of other species of *Leptothorax* in bogs indicates either that few *duloticus* females ever come to bogs in search of *Leptothorax* nests, or that the *Leptothorax* species are usually able to defend their colonies against invasion by *duloticus* females. Thus, it is likely that very few bog colonies of *Leptothorax* will be found enslaved by *duloticus*.

Probably, the *ambiguus* colony represented a small colony segment which the *duloticus* female was able to subdue. Many of the *Leptothorax* collections in the bogs apparently represented only segments of the actual colonies. Such detached sections of colonies are often without queens and may have only a few workers protecting the brood. These would seem to be rather easily captured by *duloticus* females. The female has only to overcome a few workers in one of these colony outposts and protect the entrance from workers from other parts of the colony. The developing brood would, thus, upon maturation consider the *duloticus* female to be their queen. This explanation, which is designed only for the bog collection, would seem to be the most likely explanation for colony-founding in upland communities as well. It is possible, of course, that the *duloticus*

females subdue segments of colonies in which a queen and perhaps many workers are present, but their chances for success in this situation must be small.

LASIUS MINUTUS Emery.   It has been assumed for many years that the *minutus* female establishes her colony as a social parasite in nests of species of *Lasius* (subgenus *Lasius*).   Tanquary (1911, pp. 300-302) introduced 88 *minutus* females into colonies of *Lasius* and *Acanthomyops* spp. and obtained a single adoption by a fragment of a *Lasius alienus* colony.   Creighton (1950, p. 421) cited "*Lasius alienus americanus?*" (probably *L. alienus, sensu* Wilson, 1955) as the temporary host of *minutus*. Creighton has informed me (*in litt.*) that his supposition was based upon Tanquary's study.   Wilson (1955, p. 182) cited a single collection of *minutus* which apparently was taken with *alienus* in a hickory stem; this record of association appears to be unique.

Tanquary (1911, pp. 301-302) mentioned the following conditions as suggesting a parasitic mode of colony-founding for *minutus*: 1) sporadic distribution of the species; 2) large number of females produced per colony; 3) small size of the females; 4) absence of records of independent colony-founding; and 5) mimetic coloration of females.

Our knowledge of the distribution of this ant has improved little since 1911.   There appears to be a sporadic distribution, but that this is due to social parasitism is questionable.   Rather, I believe the evidence more clearly shows that it is primarily the result of adaptation to an environment that most myrmecologists have avoided or overlooked.   Examination of marshes and swamps in northeastern United States and southeastern Canada will probably show that *minutus* is of frequent occurrence and has a considerable population density.

The production of large numbers of females is an innate characteristic of many species of *Lasius*, including some that are non-parasitic.   The alate population seems to be proportional to the worker population, and, since *minutus* may have up to several hundred thousand workers per mound, there would likely be many thousands of alates developed.   It is possible that parasitic species have a higher ratio of alates to workers than non-parasitic species, but this problem has never been investigated.

The small size of the female (compared to the size of females of other species of *Lasius*) makes it appear unlikely that one could establish a colony independently.   On this basis, and in the absence of any records of independent colony-founding, Tanquary was probably justified in drawing his conclusion.   The fact that the *minutus* female is the same color and approximately the same size as an *alienus* worker may also contribute to parasitism on *alienus* colonies.

It is, however, another matter to assume that the female must always start her colony in a nest of *alienus*.   For several reasons I doubt that this occurs very often.   First, the different habitat preferences of the two species mentioned by Wilson (1955, pp. 84-85, 182), lead one to conclude

that mature nests of *minutus* and *alienus* do not often co-exist in the same habitat. The truth of this has become strikingly apparent in the course of the present study. Approximately 700 mounds of *minutus* were found in a ten acre section of swamp and marsh southwest of Hidden Lake (Kannowski, 1959). Most of these nests occurred in the marshy areas between the larch swamp and the upland forest, and in ecotones between swamp and marsh. These are precisely the areas in which *alienus* is uncommon. *Lasius minutus* is largely absent in dense growths of larch and in a large area of fallen dead larch trees southwest of Hidden Lake, areas in which *alienus* is more frequent. I made no attempt to count all of the *alienus* nests in this same area, but probably no more than 40 to 50 occur there. On the Reserve, *alienus* most frequently occurs in the upland forests, a habitat in which I found *minutus* only once (and that nest was only about three meters away from the swamp). If *minutus* is parasitic on *alienus*, its chances for success are slender because of the sparse *alienus* population in marshy areas.

A second reason for doubting the supposed association between *minutus* and *alienus* is that the nests of the latter species are almost always found in decaying wood. In this study, all of the nests of *alienus* that were found in areas occupied also by *minutus* were in wood. *Lasius minutus*, on the other hand, mainly occupied mounds composed entirely of soil; relatively few colonies were found in soil mounds built around logs or stumps. Lastly, since both of these ants are quite abundant in their proper habitats, it would be reasonable to expect to find dealate females or incipient colonies of *minutus* in nests of *alienus*, at least occasionally, if the former regularly parasitized the latter. Not a single instance, however, has been turned up in the present study, despite intensive searching. If social parasitism is of common occurrence in *minutus*, surely one or more mixed colonies would have been found.

If parasitism upon colonies of *alienus* is rare, some other method of propagation must be used. Study of the extensive population of *minutus* near Hidden Lake suggests that there may be two distinct, but very similar, methods of colony-founding. The first hypothesis is based upon the spatial relations and structure of the nests. In the swamps and marshes of this area, nests often occur in groups of two or more. I have recently shown that these grouped nests are often components of the same colony (Kannowski, 1959). *Lasius minutus* occasionally forms outposts along its underground passageways. These outposts are very small mounds, approximately 8 to 25 centimeters high, which apparently provide protection for the root aphids which are commonly more abundant here than in the tunnels. Such mounds could easily be increased in size and utilized permanently by a part of the colony and then, either remain a segment of the original colony, or become independent. In mature colonies it is quite probable that multiple queens exist, and it is possible that one or several queens may move into one of these outposts. If this should occur, the queen or queens would almost certainly be accompanied

by a segment of the worker population, thus establishing a potentially independent colony.

The second hypothesis results from the finding of a number of dealate females in winter and spring in separate chambers just beneath the surface of two separate *minutus* mounds; there were neither workers nor brood with them. These chambers may have been connected to the rest of the nest chambers, although it was impossible to determine this accurately at the time. Now, the functional queens of the colony would not be located in such an exposed position at this time of the year, so it must be assumed that they were not colony queens. Their presence should have been known to the workers of the colony the previous fall, for *minutus* workers usually are very active in late fall, and frequently rebuild the top of the nest at that time. It would surely be known in the spring, for the females would not be likely to leave the nests in early spring because the spring floods usually cause the surfaces of the swamps and marshes to be covered with several inches of water, thus isolating the mounds. What happens after spring arrives is not known. Perhaps these females stay in their chambers, raise the first workers, and then move to find a new nesting site. This possibility seems unlikely, because it is reasonably certain that the first brood would not have developed, and hence, the new colony could not have moved, prior to the flight season of the established colony. These females and their brood would certainly be in the way at this time.

A second possibility is that the *minutus* females bury themselves in soil mounds in a manner similar to the females of *speculiventris*. They may acquire the nest odor during fall and winter and be accepted into the colony by spring. Attacking mounds of the same species is unusual, but perhaps results from an attraction to conditions similar to the nest in which the females were raised. This suggests that *minutus* females seek soil mounds, not nests in wood. If this is the case, *minutus* females may be parasitic on nests of *L. sitkaensis*, which is the only mound-forming representative of the subgenus *Lasius* in this region.

The dense *minutus* population at Hidden Lake may be explained as resulting from colony division and from utilization of existing mounds of the same species as colony-founding sites. However, neither of these processes will account for the initial colonization of the area or for the present occurrence of widely scattered *minutus* colonies in several communities at Mud Lake. The only apparent recourse to account for these is to accept the theory that *minutus* is at least occasionally parasitic on colonies of species of the subgenus *Lasius*.

LASIUS SPECULIVENTRIS Emery. In contrast to the lack of clear evidence of social parasitism in the bogs on the part of *minutus* and *umbratus*, the behavior of the females of *speculiventris* is definitely parasitic. Assuming that *minutus* is a social parasite, *speculiventris* may be considered a social hyperparasite.

Lasius speculiventris apparently must also be parasitic on some species other than *minutus*. Talbot (quoted by Wilson, 1955, p. 173) has found this ant nesting in upland forest and dry pasture communities in Illinois, where *minutus* probably rarely, if ever, occurs. Such communities are likely to be occupied by *umbratus*, which is probably an alternate host for *speculiventris*.

The colony-founding behavior of *speculiventris* females is very similar to that of females of *Lasius subumbratus* Viereck, which were observed invading colonies of *L. sitkaensis* at Cloudcroft, New Mexico, by Wheeler (1917). Two aspects of behavior are common to these two social parasites: 1) the females sometimes openly enter the host colony, with the host workers vigorously defending their nest; and 2) the females sometimes secrete themselves inconspicuously in some portion of the host nest, presumably to gain the nest odor and later enter the nest chambers.

This similarity of behavior may be an indication of close phylogenetic relationship. The probable relationships of these species have apparently never been determined; however, both species are included in the subgenus *Chthonolasius* and morphologically resemble *umbratus* much more so than *minutus*. If *speculiventris*, *subumbratus*, and *umbratus* are closely related species, their methods of colony-founding may be similar.

LASIUS UMBRATUS (Nylander). It has long been known that European representatives of *L. umbratus* establish their colonies in the nests of *L. niger* and *L. alienus* (Crawley, 1909; Crawley and Donisthorpe, 1913; Donisthorpe, 1927; Gösswald, 1938; Hölldobler, 1953). However, there is little conclusive evidence to show that our North American *umbratus* females establish their colonies in the same way. Gregg (1944, footnote, p. 471) cited three records of *umbratus* females being found in nests of "*Lasius niger alienus americanus*" and "*Lasius niger neoniger*." Probably all three hosts are *Lasius alienus* (*sensu* Wilson, 1955). Buren (1944, p. 297) recorded a dealate female of *umbratus* in a small colony of "*Lasius flavus nearcticus*." Two mixed colonies of *niger* and *umbratus*, and one of *alienus* and *umbratus* are recorded by Wilson (1955, p. 164). This author introduced dealate females into colonies and colony fragments of *Lasius sitkaensis*, *alienus*, and *neoniger*, but was unsuccessful in obtaining a complete adoption. He suggested that *umbratus* females may join recently mated females of the host species (which has been demonstrated by Hölldobler's (1953) experiments with European *umbratus* and *niger* females). However, Wilson's attempts to get *umbratus* and *neoniger* females to nest together failed, probably, as he stated, because *neoniger* is not a natural host of *umbratus*. Such a result might have been anticipated, since Wilson himself noted that in northeastern United States *umbratus* occurs in moist woodland, while in the same region *neoniger* is absent from these communities (1955, pp. 101-103, 162).

Wilson (1955, p. 164) suggested "on what admittedly constitutes negative evidence, that behavior in the population I studied may differ

from that in the European populations." Certainly, for an ant that is as abundant in various parts of North America as is *umbratus*, one might expect to find more evidence of a parasitic colony-founding behavior, if such exists. Perhaps this ant has other methods of establishing colonies.

Most of the records of *umbratus* from the bogs are based upon dealate females found without brood in May of 1953 and of 1956 in small chambers in the soil under moss at the bases of trees in the deciduous hardwood swamps. Despite intensive search I could not find any incipient colonies later in the summer. I have also found dealate females in independent chambers in various upland forest communities. These observations are similar to those described by Wheeler (1917, p. 169) for *umbratus*. Two possible explanations of these occurrences are here suggested: 1) these dealate females are capable of founding colonies independently. 2) These females are incapable of founding colonies independently, and are found solitary because they either are unable to find or do not seek a suitable host colony in the fall; they then overwinter in a cavity and in the spring seek a host colony.

A careful study of the colony-founding behavior of this ant in North America is much needed.

2. **Pleometrosis**.—The joining together of two or more females of the same species to establish a colony has been termed pleometrosis (Wasmann, 1910). Apparently, this is of rare occurrence in the bogs, for it was observed of *Myrmica brevinodis* only. Wheeler (1910, p. 190) advanced the hypothesis that pleometrotic colonies resulted from two or more "sisters" from the same colony meeting in the air after copulation and descending to the earth to form a single colony together. It seems to me that the probability of this happening is rather small (except in mass flights and swarms), and that a more likely explanation is available. I believe that it is more probable that pleometrosis usually results from intranidal mating with females from the same colony (and possibly, from different colonies) joining together to start a colony at a new site.

The occurrence of mature polygynous colonies is, I think, less often the result of pleometrosis than of intranidal matings. This seems probable because polygynous colonies are most common at the end of the flight season (8). Several to many dealate females were found in colonies of *Ponera pennsylvanica*, *Myrmica* spp., *Leptothorax ambiguus*, *Tapinoma sessile*, and *Dolichoderus pustulatus*, and they may occur in colonies of some of the other species. Mating apparently takes place occasionally

(8) Haskins and Enzmann (1938, p. 154) suggested that the occurrence of many dealate females in nests of *Ponera* and *Amblyopone* (= *Stigmatomma*) at the end of the flight season is the result of females returning to their own nest after flight. I cannot deny this as a possibility at least for some species, but there have been no direct observations in support of this hypothesis. Its occurence would be most likely in the case of species which swarm or mate directly above the nest (see Kannowski and Kannowski, 1957, p. 374), but would be very unlikely in the case of *Dolichoderus*, *Tapinoma*, and *Lasius* spp., alates of which fly far away from the nests.

in the nests of *Myrmica fracticornis* and *Tapinoma sessile*, and probably also in nests of some of the others.

3. **Habitat selection**.—Although many thousands of alates fly from nests in an area such as one of these bogs, few dealate females are found after a flight. Most of these are found in the "usual" habitat. Undoubtedly there is a high mortality during flights due to spiders, birds, and predacious insects (especially dragonflies). Many females may drop to environments in which they are unable to survive. However, the occurrence of colony-founding females primarily in environments normally inhabited by the species may indicate that they respond to environmental conditions similar to those of the habitat from which they came.

Habitat selection may be considered in two phases: macrohabitat selection and microhabitat selection. In the former the alate female orients herself to a major environment such as a field, a forest, or a desert, etc. Here, visual orientation would be important, but it is possible that alates perceive differences in temperature and humidity as well. Evidently alates of some species do not exhibit any macrohabitat orientation. This is exemplified by certain alates which fall to the ground *in copula*. After copulation has been completed, the females immediately break off their wings and start looking for a site in which to establish a colony.

On the ground the female begins the process of microhabitat selection. Brian (1952) has suggested the importance of visual orientation in this process. However, for some species at least, visual sitmuli may not be very effective at this level (see Kannowski and Kannowski, 1957, p. 374). Certainly contact with the substrate must be very important, for this is indicated by the attraction of *Lasius* females to soil mounds in the bogs. It is also possible that females are attracted by odors, sounds, temperature, and moisture. Probably, a combination of several factors is important for most species.

Summary.

The flight activities and colony-founding behavior of the ants inhabiting three bogs in southeastern Michigan were studied. The time of the year that alates occur in the nests is given for most of the species (Table I), and the flights of eight species are described. *Myrmica fracticornis* flights occur in early evening from mid-July to early August. Flights commence at this time evidently because the alates are stimulated by decreasing light intensities. Flights of *Tapinoma sessile* take place in mid-morning from late June to mid-July. The flight period for this species is largely influenced by temperature. Flights of three species of *Dolichoderus* (*mariæ*, *plagiatus*, and *pustulatus*) were observed in the bogs. *Dolichoderus* flights always begin in early morning and are influenced mainly by temperature. The flights of two species of *Lasius* (*minutus* and *speculiventris*) were seen during afternoons in late August. Alates of these two species avoid direct sunlight, so that flights occur only when the nests are

shaded. The single *Formica fusca* flight seen in the bogs took place about mid-morning in mid-July.

Flights may be fitted into three categories on the basis of size. *Sparse flights* are those in which the alates fly at an average rate of two or less per minute. In the bogs *Myrmica fracticornis*, *Dolichoderus plagiatus*, *Dolichoderus pustulatus*, and *Formica fusca* had sparse flights. An average rate of 5 to 40 alates flying per minute is characteristic of *moderate flights*, which were observed of *Tapinoma sessile* and *Dolichoderus mariae*. An average rate of 100 or more alates flying per minute constitutes a *mass flight*. *Lasius minutus* and *Lasius speculiventris* had mass flights in the bogs.

The regularity of flight occurrence is another species characteristic. The daily occurrence of flights from each mature colony throughout the flight season (except for bad weather) is a type of behavior which I have called *continuous flights*. In the bogs only *Dolichoderus mariae* colonies showed this type of behavior consistently. Flights from one large colony of *Tapinoma sessile* were also continuous, but those of smaller colonies of this species were not. Flights of a species which take place daily in an area, but usually at intervals of several days from individual colonies, are termed *discontinuous flights*. Flights of *Myrmica fracticornis*, *Dolichoderus plagiatus*, *Dolichoderus pustulatus*, and *Formica fusca* were of the discontinuous type, as were those of most colonies of *Tapinoma sessile*. Flights of certain species evidently do not take place until most, if not all, alates have emerged from the pupal cases. Once these flights start, they may occur daily, if the climatic conditions are favorable. Flights of this kind are called *accumulated flights*. They were exhibited in the bogs by *Lasius minutus* and *Lasius speculiventris*.

Females of most of the bog species establish their colonies independently, but several are social parasites. Beginning their colonies independently are species of *Ponera*, *Myrmica*, *Stenamma*, *Leptothorax* (all except *L. duloticus*), *Crematogaster*, *Tapinoma*, *Dolichoderus*, *Camponotus*, *Lasius* (*alienus*, and apparently also *umbratus*), and *Formica* (*fusca* and *neorufibarbis*). Colony-founding females which overwinter without brood include those of *Ponera pennsylvanica*, *Crematogaster cerasi*, and the three species of *Dolichoderus*. Taxa in which larvæ are overwintered in addition to the queen include *Myrmica*, *Leptothotax*, *Lasius*, and *Formica*. Workers mature in the colonies of *Tapinoma* and *Camponotus* during the same summer that the colony is started. Some *Lasius minutus* colonies may be formed by colony division. *Leptothorax dulotieus* and *Formica ulkei* are social parasites, their respective hosts being *Leptothorax ambiguus* and *Formica fusca*. The females of *Lasius minutus* are presumed to be social parasites with *Lasius alienus* being a possible host. *Lasius speculiventris* is evidently a social hyperparasite, being parasitic on colonies of *Lasius minutus*. Females of *Lasius speculiventris* gain entrance to *Lasius minutus* colonies either by forcing their way past the workers into an opening or by forming a chamber beneath the surface of the mound.

Résumé.

Dans ce travail on a étudié les mouvements de vol et le comportement de fondation de la colonie chez les fourmis qui habitent les marais du sud-est de Michigan. La période où les sexués ailés se trouvent dans les nids est indiquée pour la plupart des espèces (Tableau 1), et les vols de huit espèces sont décrits. Le vol de *Myrmica fracticornis* a lieu très tôt dans la soirée de mi-juillet jusqu'au début d'août. Cette période de départ des vols est liée directement à la diminution de la lumière. Le vol de *Tapinoma sessile* a lieu au milieu de la matinée de la fin juin jusqu'à la mi-juillet. La durée du vol de cette espèce est très influencée par la température. Les vols de trois espèces de *Dolichoderus* (*mariae*, *plagiatus* et *pustulatus*) ont été observés dans les marais. Le vol de *Dolichoderus* commence toujours le matin de bonne heure et il dépend surtout de la température. Les vols de deux espèces de *Lasius* (*minutus* et *speculiventris*) ont été observés dans les après-midi des derniers jours d'août. Les sexués ailés de ces deux espèces fuient la lumière directe du soleil ; ainsi le vol n'a lieu que lorsque les nids se trouvent à l'ombre. Le seul vol de *Formica fusca* observé dans les marais a eu lieu au milieu de la matinée à mai-juillet.

Suivant le nombre de sexués ailés participant aux vols, ceux-ci se classent en trois catégories. *Sparse flights* : ceux où l'on observe deux ou moins de sexués ailés en vol minute. Dans les marais *Myrmica fracticornis*, *Dolichoderus plagiatus*, *Dolichoderus pustulatus*, et *Formica fusca* présentaient des *sparse flights*. Un nombre moyen de cinq à quarante sexués ailés par minute caractérise les *moderate flights* opérés par *Tapinoma sessile* et *Dolichoderus mariae*. Un nombre moyen de cent ou plus de sexués ailés par minute constitue un *mass flight Lasius minutus* et *Lasius speculiventris* présentant ce comportement dans les marais.

La régularité des vols est une autre caractéristique de chaque espèce. Les vols journaliers de chaque colonie mûre pendant la saison des vols (sauf par mauvais temps) sont caractéristiques d'un comportement que j'ai nommé *continuous flights*. Dans les marais, seules les colonies de *Dolichoderus mariae* ont manifesté uniformément ce comportement. Les vols d'une grande colonie de *Tapinoma sessile* étaient aussi *continuous flights*, tandis que les vols de toutes les autres colonies de cette même espèce ne l'étaient pas. J'ai nommé *discontinuous flights* ces vols qui ont lieu tous les jours dans un terrain, mais qui ont lieu d'habitude à des intervalles de plusieurs jours dans les colonies séparées. Les vols de *Myrmica fracticornis*, *Dolichoderus plagiatus*, *Dolichoderus pustulatus*, et *Formica fusca* étaient du type *discontinuous flights*, aussi bien que ceux de la plupart des colonies de *Tapinoma sessile*. Les vols de certaines espèces ne commencent évidemment que lorsque la plupart des sexués ailés, sinon tous, sont sortis des cocons. Dès que ces vols ont commencé, ils peuvent avoir lieu tous les jours par un temps favorable. Les vols de ce type sont nommés *accumulated*

flights, caractéristiques, dans les marais, des espèces de *Lasius minutus* et *Lasius speculiventris*.

Les femelles de la plupart des espèces observées dans les marais établissent leurs colonies indépendamment, mais plusieurs sont des parasites sociaux. Parmi les premières, citons *Ponera, Myrmica, Stenamma, Leptothorax* (sauf *L. duloticus*), *Crematogaster, Tapinoma, Dolichoderus, Camponotus, Lasius* (*alienus*, et apparemment aussi *umbratus*) et *Formica* (*fusca* et *neorufibarbis*). Les femelles qui passent l'hiver sans couvain comprennent les espèces de *Ponera pennsylvanica, Crematogaster cerasi* et les trois espèces de Dolichoderus. Les genres où la reine et les larves passent l'hiver comprennent *Myrmica, Leptothorax, Lasius* et *Formica*. Les ouvriers mûrissent dans les colonies de *Tapinoma* et *Camponotus* au cours du même état où la colonie a été établie. Certaines colonies de *Lasius minutus* peuvent se former par division. *Leptothorax duloticus* et *Formica ulkei* sont des parasites sociaux dont les hôtes respectifs sont *Leptothorax ambiguus* et *Formica fusca*. Il faut présumer que les femelles de *Lasius minutus* sont des parasites sociaux dont *Lasius alienus* est l'hôte possible. *Lasius speculiventris* est évidemment un hyperparasite sociaux, parasite des colonies de *Lasius minutus*. Les femelles de *Lasius speculiventris* pénètrent dans les colonies de *Lasius minutus* soit en forçant l'entrée du nid, soit en creusant sous la fourmilière.

Zusammenfassung.

Beobachtet wurden die Hochzeitsflüge und die Koloniengründung der Ameisen, die in drei Mooren im südöstlichen Teile von Michigan zu finden waren. Die Jahreszeiten der Auftreten der geflügelten Geschlechtstiere in den Nestern werden für die meisten Arten angegeben (Tabelle I) und die acht verschiedenen Typen von Hochzeitsflügen beschrieben. Die *Myrmica fracticornis*-Flüge finden am frühen Abend von der Mitte Juli bis zum frühen August statt. Die Flüge fangen augenscheinlich zu dieser Zeit an, weil die Geschlechtstiere durch abnehmende Lichtstärke angereizt werden. Die *Tapinoma sessile*-Flüge finden in der Mitte des Vormittags statt. Die Flugeszeit dieser Art wird zum grossen Teil durch die Temperatur beeinflusst. Die Flüge von drei *Dolichoderus*-Arten (*mariae, plagiatus* und *pustulatus*) wurden in den Mooren beobachtet. Die *Dolichoderus*-Flüge beginnen immer früh am Morgen und werden hauptsächlich durch die Temperatur beeinflusst. Die Flüge von zwei *Lasius*-Arten (*minutus* und *speculiventris*) wurden während des Nachmittags im späten August gesehen. Die Geschlechtstiere von diesen zwei Arten vermeiden das direkte Sonnenlicht, so dass die Flüge finden statt, nur wenn die Nester umschattet sind. Der einzige in den Mooren beobachtete *Formica fusca*-Flug fand ungefähr in der Mitte des Morgens in der Mitte Juli statt.

Die Flüge können in drei auf Grösse basierte Klassen eingeteilt werden. *Dünne Flüge* sind die, in welchen im Durchschnitt zwei oder weniger Geschlechtstiere in der Minute fliegen. In den Mooren zeigten *Myrmica*

fracticornis, Dolichoderus plagiatus, Dolichoderus pustulatus, und *Formica fusca* dünne Flüge. Eine Anzahl von fünf bis vierzig Geschlechtstiere im Durchschnitt in der Minute kennzeichnet die *mässigen Flüge*, die von *Tapinoma sessile* und *Dolichoderus mariae* beobachtet wurden. Wenn hundert oder mehr Geschlechtstiere in der Minute fliegen, hat man einen *Massenflug. Lasius minutus* und *Lasius speculiventris* zeigten Massenflüge in den Mooren.

Die Regelmässigkeit der Vorkommen der Flüge ist ein andere Eigentümlichkeit der verschiedenen Arten. Wenn regelmässige Flüge aus allen reifen Kolonien tagtäglich (ausser bei schlechtem Wetter) vorkommen, so habe ich diese als *andauernde Flüge* bezeichnet. In den Mooren haben nur *Dolichoderus mariae*-Kolonien dieses Verhalten ständig gezeigt. Die Flüge von einer grossen *Tapinoma sessile*-Kolonie waren auch andauernd, aber diejenigen von kleineren Kolonien dieser Art waren es nicht. Die Flüge, die täglich in einer bestimmten Stelle aber gewöhnlich aus einzelnen Kolonien in Zwischenzeiten von einigen Tagen stattfinden, werden *unterbrochene Flüge* genannt. Die Flüge von *Myrmica fracticornis, Dolichoderus plagiatus, Dolichoderus pustulatus*, und *Formica fusca* waren von dieser unterbrochenen Art, und so waren auch diejenigen von den meisten *Tapinoma sessile*-Kolonien. Die Flüge von gewissen Arten finden augenscheinlich nicht statt, bis die meisten, wo nicht alle Geschlechtstiere aus den Kokons herausgekommen sind. Fangen diese Flüge einmal an, so können sie täglich vorkommen, wenn das Wetter günstig ist. Solche Flüge werden als *angehäufte Flüge* bezeichnet und wurden in den Mooren von *Lasius minutus* und *Lasius speculiventris* gezeigt.

Die Weibchen der meisten Ameise-Arten in den Mooren gründen ihre Kolonien unabhängig, aber einige sind Sozialparasiten. Arten, die ihre Kolonien unabhängig gründen, sind : *Ponera, Myrmica, Stenamma, Leptothorax* (alle mit Ausnahme von *L. duloticus*), *Crematogaster, Tapinoma, Dolichoderus, Camponotus, Lasius* (*alienus*, und wahrscheinlich auch *umbratus*), und *Formica* (*fusca* und *neorufibarbis*). Die Kolonien gründenden Weibchen, die ohne Brut überwintern, umfassen diejenigen von *Ponera pennsylvanica, Crematogaster cerasi*, und die drei *Dolichoderus* Arten. Gattungen, in welchen die Königin und ausserdem die Larven überwintern, sind : *Myrmica, Leptothorax, Lasius*, und *Formica*. Arbeiterinnen reifen in den *Tapinoma*- und *Camponotus*-Kolonien während desselben Sommers, in dem die Kolonie gegründet wird. Einige *Lasius minutus*-Kolonien können vermittels Kolonieaufspaltung gegründet werden. *Leptothorax duloticus* und *Formica ulkei* sind Sozialparasiten; ihre respective Wirte sind *Leptothorax ambiguus* und *Formica fusca*. Es wird angenommen, das die *Lasius minutus*-Weibchen Sozialparasiten sind ; *Lasius alienus* sind möglicherweise die Wirte. *Lasius speculiventris* ist augenscheinlich eine Sozialhyperparasit und zwar auf den *Lasius minutus*-Kolonien. Die *Lasius speculiventris*-Weibchen dringen durch einen Eingang in die *Lasius minutus*-Kolonien an den Arbeiterinnen vorbei, oder sie machen auch eine Kammer unter der Oberfläche des Ameisenhaufens.

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LA GLANDE MANDIBULAIRE DU TERMITE A COU JAUNE (*CALOTERMES FLAVICOLLIS*)

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Chez les Termites, il existe un certain nombre de glandes exocrines céphaliques. Parmi celles-ci, les glandes mandibulaires ont été jusqu'ici fort peu étudiées. Seul Holmgren (1909) les cite brièvement dans une étude anatomique générale.

Notre étude porte sur *Calotermes flavicollis*, le Termite à cou jaune de la région de Banyuls, qui est élevé au Laboratoire d'Évolution. Les principaux fixateurs employés
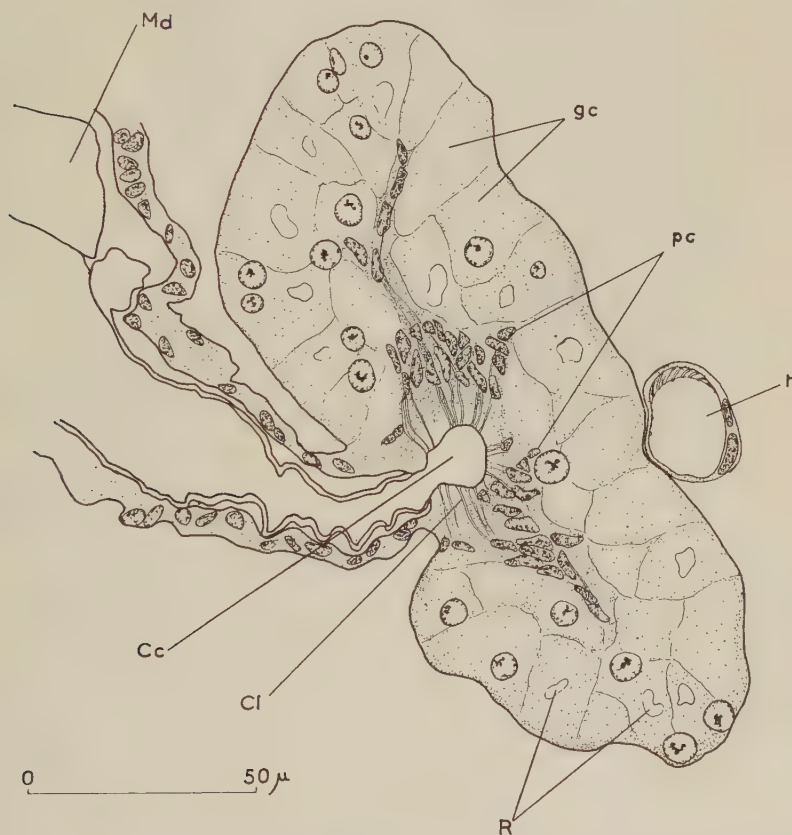
Fig. 1. — *Larve âgée.* Coupe longitudinale de la glande *(Bouin alcoolique, Prenant).*

md, mandibule ; *gc*, grande cellule ; *pc*, petite cellule ; *Cc*, canal central ; *Cl*, canalicule ; *R*, réservoir intracellulaire ; *t*, trachée.

furent les mélanges de Bouin (alcoolique et aqueux), Champy, Helly et Halmi. Les principales colorations utilisées furent la triple coloration de Prenant (après Bouin), la fuschsine anilinée d'Altmann (après Champy) avec différenciation à l'aurantia, et la réaction de Hotchkiss Mac Manus combinée à l'hématoxyline de Groat.

I. — ANATOMIE DE LA GLANDE

Nous prendrons pour faire cette étude générale une larve âgée.

1º **Morphologie générale.** (fig. 1). — La glande mandibulaire est située à la base de la mandibule, entre la mandibule et la partie latérale de la maxille. Chaque glande se compose d'une masse cellulaire de 180 à 200 microns de diamètre, légèrement aplatie, accolée à l'hypoderme.

Les cellules de la glande sont disposées autour d'un canal central de 70 microns de longueur et 10 microns de diamètre dans lequel débouchent indépendamment de nombreux canalicules par petits groupes de 10 à 20. Ce canal débouche dans le cibarium. Accolée à la glande, on trouve toujours une trachée de diamètre important.
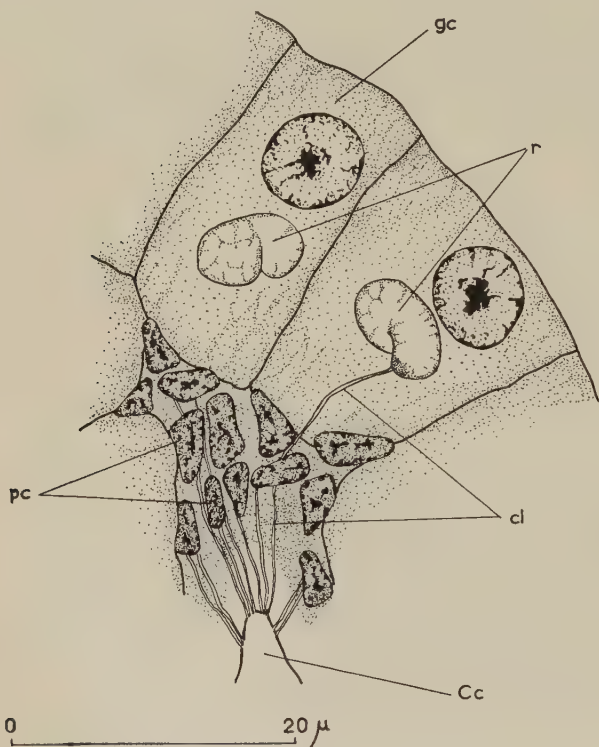
Fig. 2. — *Larve 4ᵉ stade.* Coupe transversale *(Bouin alcoolique, Prenant).*

gc, grande cellule ; pc, petite cellule ; cl, canalicule ; Cc, canal central ; r, réservoir intracellulaire.

2º **Histologie.** — On distingue deux catégories de cellules :
— des grandes cellules périphériques ;
— des petites cellules entre les noyaux desquelles on peut reconnaître les canalicules issus des grandes cellules.

1º Les *grandes cellules* sont grossièrement prismatiques ; elles mesurent environ 25 μ de hauteur et 15 μ de diamètre à leur base.
— Une *coloration de Prenant* (fig. 1 et 2) montre un cytoplasme assez

nettement basophile, au sein duquel le vert lumière colore une vacuole bien délimitée, assez allongée et souvent légèrement incurvée. Dans certains cas favorables, on peut voir les canalicules pénétrer dans les grandes cellules et aboutir à ces vacuoles.

— Par la *méthode Champy-Altmann*, les canalicules sont colorés en rouge par la fuchsine. On remarque, en outre, dans le cytoplasme, des zones
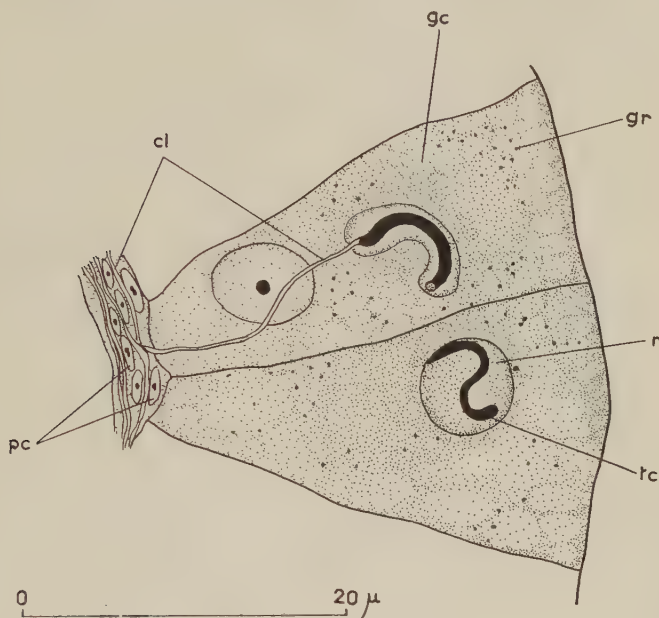

FIG. 3. — *Larve âgée*. Coupe transversale *(Champy, Fuchsine d'Altmann)*.

gc, grande cellule ; *pc*, petite cellule ; *cl*, canalicule ; *r*, réservoir intracellulaire ; *tc*, terminaison spiralée du canalicule dans le réservoir ; *gr*, granulations qui ont pris la fuchsine.
Dans la cellule supérieure, l'extrémité distale du canalicule a été sectionnée.

claires au sein desquelles on trouve un filament spiralé relié à un canalicule (fig. 3).

— La *coloration de Hotchkiss-Mac Manus* révèle également, au sein de vacuoles assez claires, un filament creux, grossièrement hélicoïdal, relié à un canalicule très colorable dans son trajet intracellulaire (fig. 4) ; l'amylase salivaire n'altère pas cette coloration.

La comparaison de ces méthodes montre donc l'existence dans le cytoplasme d'une grande vacuole que l'on peut appeler « réservoir intracellulaire » signalé par Holmgren (1909). Dans ce réservoir, le départ du canalicule est contourné. La paroi du canalicule est formée de trois parties différemment colorables : la première dans le réservoir intracellulaire contient des polysaccharides, les deux autres (dans la grande cellule et dans la région des petites cellules) semblent être de nature cuticulaire, sans que les réactions employées permettent d'affirmer qu'elles soient chitineuses.

2º LES PETITES CELLULES, aux limites indistinctes, sont localisées autour du canal central et en quelques travées qui pénètrent entre les grandes cellules (fig. 1). Le cytoplasme de ces cellules est réduit, leurs noyaux allongés et riches en matériel chromatique. Par ces caractères, les petites cellules
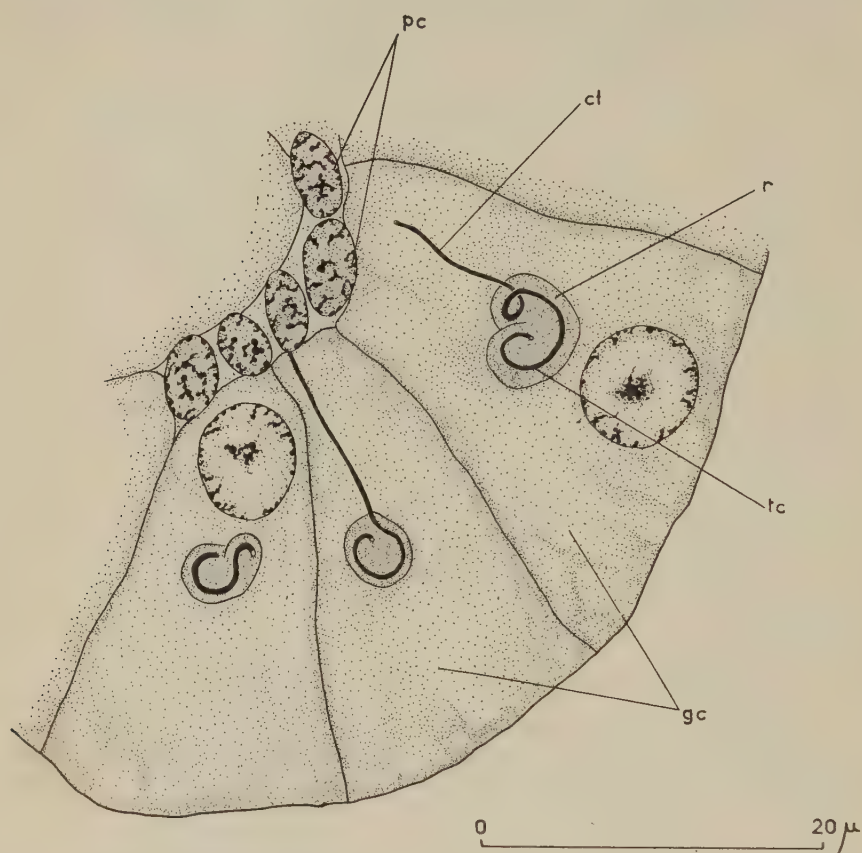

FIG. 4. — *Larve âgée*. Coupe transversale *(Helly, Hotchkiss-Mac Manus)*.

gc, grande cellule ; *pc*, petite cellule ; *cl*, canalicule ; *r*, réservoir intracellulaire ; *tc*, terminaison du canalicule.

Les canalicules sont assez nettement Hotchkiss positifs dans les grandes cellules.

ressemblent aux cellules hypodermiques banales. Les canalicules précédemment décrits traversent la zone des petites cellules sans qu'il soit possible de savoir s'ils passent entre ces cellules ou à leur intérieur.

La glande mandibulaire est donc formée de deux types de cellules nettement distincts. Nous avons cherché à préciser la signification de cette dualité cellulaire et l'origine des canalicules, en étudiant d'une part, les modifications de la glande au cours de la mue, d'autre part, le développement post-embryonnaire de la glande, ce qui nous a conduit à envisager également ses variations dans les différentes castes.

II. — ÉVOLUTION DE LA GLANDE AU COURS DE LA MUE

1° **Description des phénomènes.** — 1° Avant le rejet de l'exuvie. — a. *Rejet des canalicules et début de leur reconstitution.* — Au moment où la cuticule commence à se décoller de l'hypoderme, le revêtement du canal central de la glande se décolle également. Mais les canalicules restent soli-
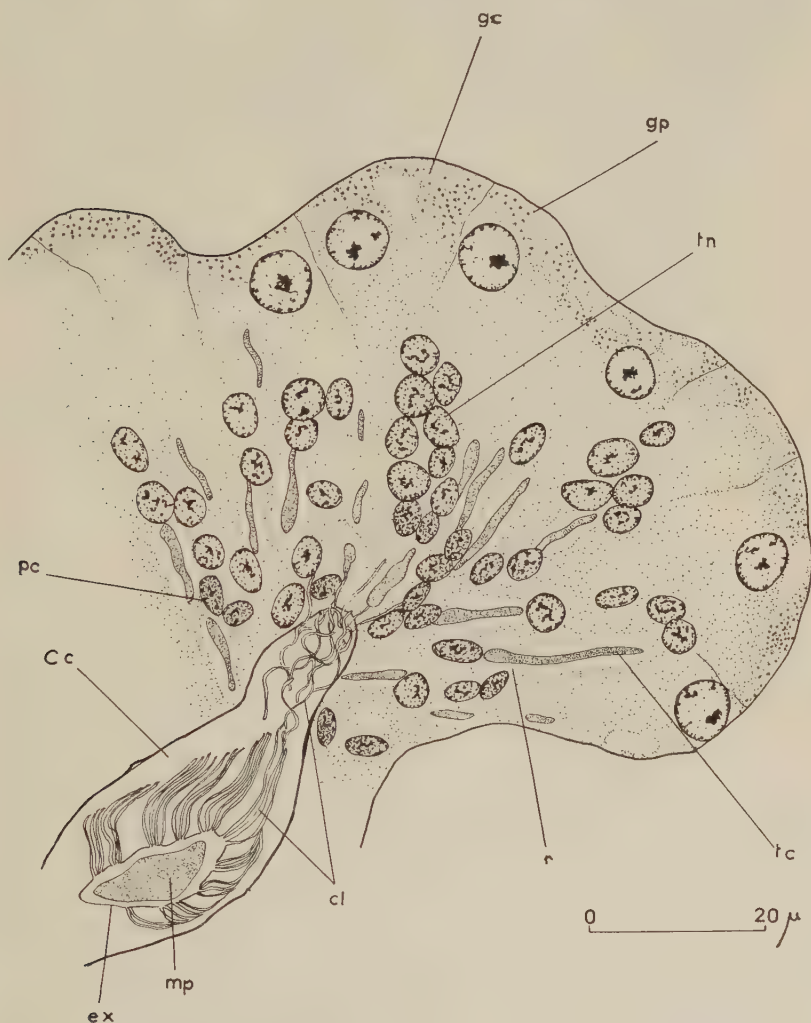

Fig. 5. — *Larve âgée* (avant la mue). Coupe transversale *(Helly, Hotchkiss-Mac Manus).*

gc, grande cellule ; *pc*, petite cellule ; *Cc*, canal central ; *cl*, canalicule ; *tc*, terminaison du canalicule ; *r*, réservoir ; *tn*, travées de noyaux centrifuges ; *gp*, granulations Hotchkiss positives *ex*, exuvie ; *mp*, masse Hotchkiss positive.
Les terminaisons des canalicules émigrant vers le canal central, le développement de travées de noyaux centrifuges.

daires de la cuticule et suivent l'exuvie dans le canal axial de la glande en y formant un chevelu. Les terminaisons intracellulaires des canalicules deviennent plus épaisses, se déspiralisent, tandis qu'elles progressent vers le canal central, entourées d'une zone claire résultant peut-être de l'allongement du réservoir (fig. 5).

A un stade un peu plus tardif, on trouve dans la lumière de la glande les canalicules complets avec leurs terminaisons intracellulaires (fig. 6). A ce moment, on ne voit dans la glande elle-même aucun élément du canalicule. La striation du cytoplasme autour du canal central représente peut-être la trace des canalicules.

Juste avant le rejet de l'exuvie (fig. 7), la partie proximale des canalicules est reconstituée, en continuité avec la nouvelle cuticule. Dans les cellules, la coloration de Hotchkiss-Mac Manus teinte faiblement un filament mal individualisé au sein d'un réservoir peu distinct. (A ce
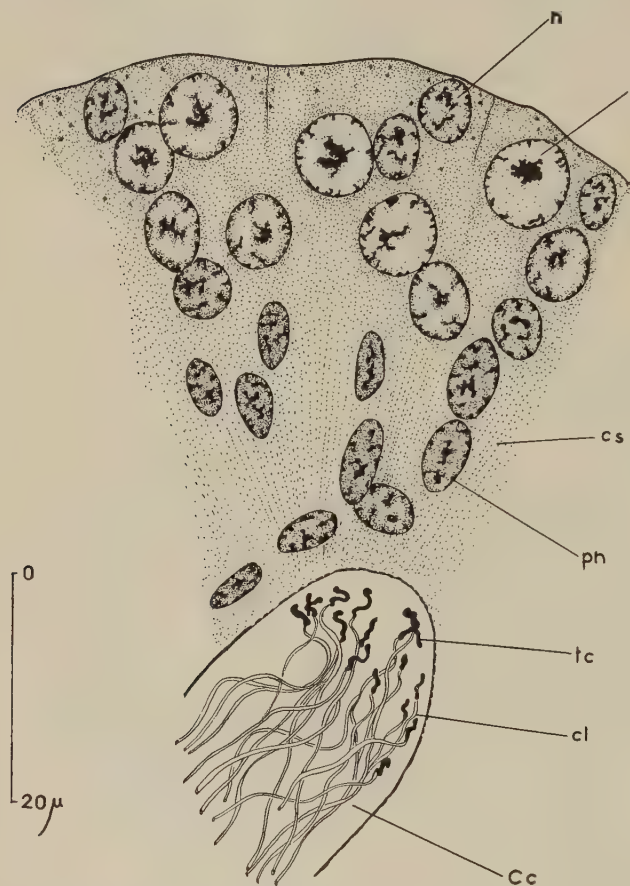
Fig. 6. — *Larve âgée* (avant la mue). Coupe transversale *(Helly, Hotchkiss-Mac Manus)*. Les canalicules sont rejetés en entier.

gn, gros noyaux ; *pn*, petits noyaux ; *n*, noyaux intermédiaires ; *Cc*, canal central ; *cl*, canalicules ; *tc*, terminaisons des canalicules ; *cs*, cytoplasme strié.

moment, les canalicules rejetés sont encore dans le canal central.) Notons que, pendant ces phénomènes, les limites cellulaires sont devenues floues.

b. *Évolution des cellules*. — Les grandes cellules périphériques ne changent pas (mis à part la disparition du réservoir et du canalicule) ; au contraire, dès le début, on constate la formation de travées radiaires de petites cellules ; les limites cellulaires étant indiscernables, on observe, en fait, des lignes de noyaux rayonnants à partir du canal axial ; ces noyaux

sont de plus en plus gros vers la périphérie, plus arrondis que les petits
noyaux centraux, et leur matériel chromatique devient moins dense
(fig. 5). Par la suite, ces noyaux intermédiaires se répartissent dans toute
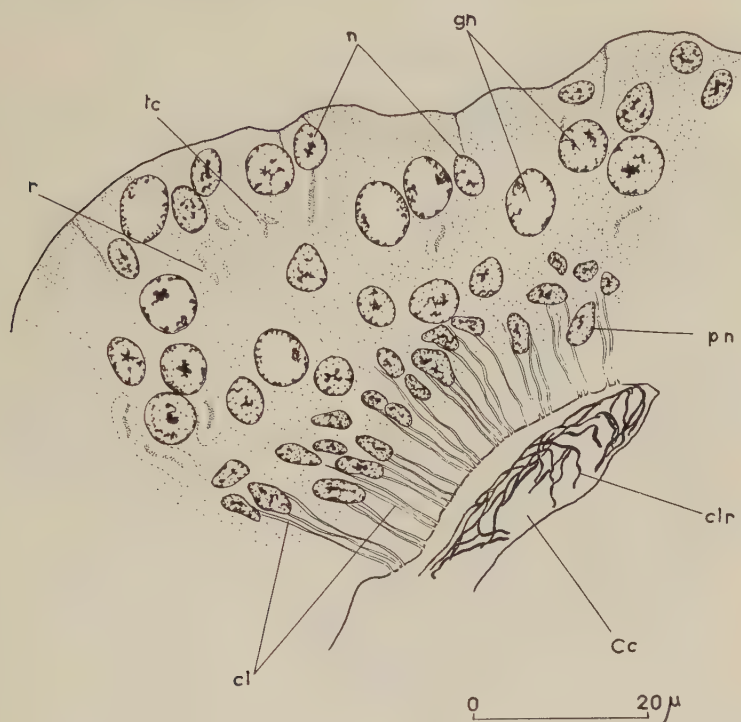la glande jusqu'à la périphérie. Il y a donc une migration centrifuge de

Fig. 7. — *Larve âgée* (juste avant la mue). Coupe transversale *(Helly, Hotchkiss-Mac Manus)*.
Début de la reconstitution des canalicules.

gn, gros noyaux ; *pn*, petits noyaux ; *p*, noyaux intermédiaires ; *cl*, canalicules ; *clr*, canalicules
rejetés ; *tc*, terminaison des canalicules ; *r*, réservoir ; *Cc*, canal central.

noyaux qui se différencient à partir des petites cellules, tandis que les cana-
licules sont rejetés et que des nouveaux canalicules se différencient.

2° Après le rejet de l'exuvie. — a. *Fin de la reconstitution des cana-
licules*. — Dès le lendemain de la mue, les canalicules sont parfaitement
visibles, aussi bien dans les grandes cellules, qu'à leur raccord avec le canal
central. Il semble donc qu'ils soient très rapidement reconstitués (fig. 8).

b. *Évolution des noyaux*. — Dans le jour qui suit la mue, les noyaux de
dimension moyenne sont répartis dans toute la glande.

Au deuxième jour après la mue, on distingue trois sortes de noyaux
(fig. 8) :

— les gros noyaux des cellules périphériques (7 μ de diamètre) qui n'ont
jamais changé d'aspect ;

— les petits noyaux (4 à 5 μ de longueur) localisés autour du canal central ;

— des noyaux intermédiaires (5 μ de longueur) qu'on ne rencontre plus qu'à la périphérie ; l'observation attentive semble indiquer que *chacun* de ces noyaux est contenu à l'*intérieur* d'une grande cellule sécrétrice.
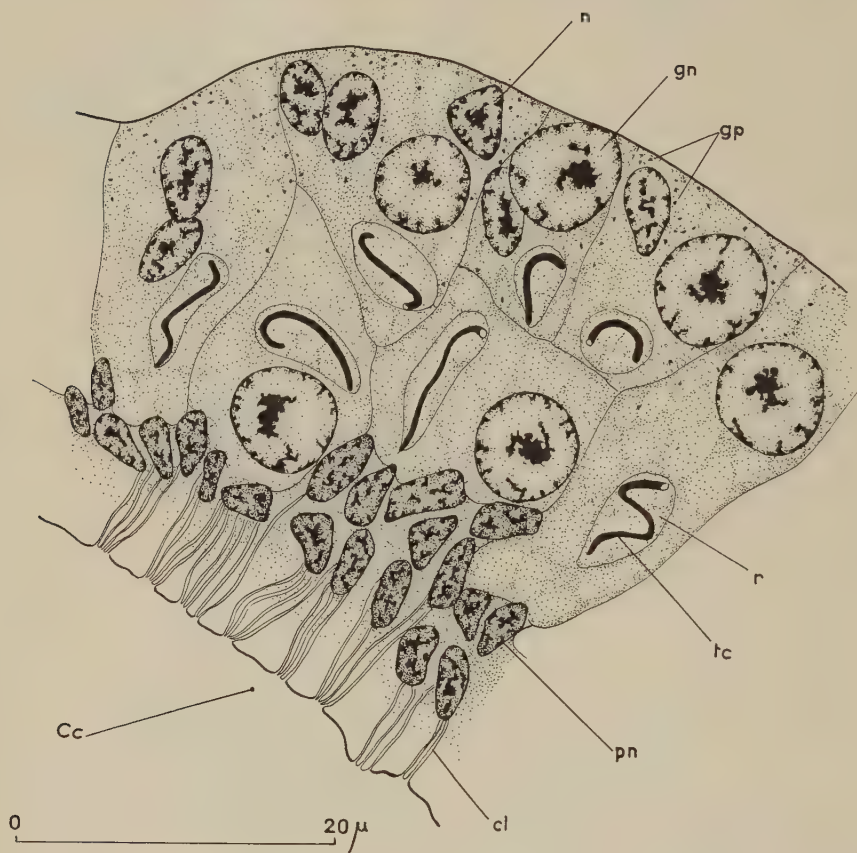

Fig. 8. — *Larve âgée* (deux jours après la mue). Coupe transversale *(Bouin, Hotchkiss-Mac Manus)*.

gn, gros noyaux ; *pn*, petits noyaux ; *n*, noyaux intermédiaires ; *cl*, canalicules ; *t*, terminaison du canalicule ; *r*, réservoir ; *Cc*, canal central ; *gp*, granulation Hotchkiss positive.

Au troisième jour, les noyaux intermédiaires sont presque tous en dégénérescence sous forme de masses compactes colorées par l'hématoxyline (fig. 9).

Au quatrième jour, il n'y a plus que quelques-unes de ces boules sidérophiles. Enfin, le cinquième jour, la glande a repris son aspect d'intermue : il n'y a plus que deux types de cellules.

2° ***Interprétation.*** — Nous pensons pouvoir reconstituer ainsi le déroulement des phénomènes : lors de la mue, les canalicules restent en

continuité avec l'ancienne cuticule et sont rejetés en totalité, y compris la portion contenue dans le réservoir des cellules sécrétrices ; le réservoir lui-même disparaît, et une partie au moins de sa substance est rejetée avec la partie distale des canalicules. A cela près, les cellules sécrétrices périphé-riques ne montrent pas de modifications histolo-giques.

La reconstitution des canalicules procède en direction centrifuge et s'accompagne d'une migration concomittante des petites cellules centrales ; nous sommes en droit de penser que ces petites cellules sécrètent les canalicules au fur et à mesure de leur migration ; il semble même que la petite cellule migrante pénètre à l'intérieur d'une grande cellule sécrétrice et sécrète ainsi la partie distale du canalicule ; le processus étant achevé, la petite cellule dégénère.

Les petites cellules groupées autour du canal central apparaissent ainsi comme des cellules de réserve, chargées de reconstituer à chaque mue les canalicules des cellules sécrétrices, qui restent en place. Ainsi, une proportion notable de petites cellules dégénère lors de la mue, et l'on doit observer une multiplication compensatrice de ces cellules ; malheureusement, les mitoses, chez le Termite, ont lieu longtemps avant l'exuviation proprement dite, alors que rien extérieurement n'indique la mue prochaine ; ce fait, joint à la durée variable (mais toujours longue) des intermues, rend l'observation de ces mitoses aléatoire. Nous avons eu pourtant la chance de l'observer à deux reprises, chez des nymphes à courts fourreaux alaires ;
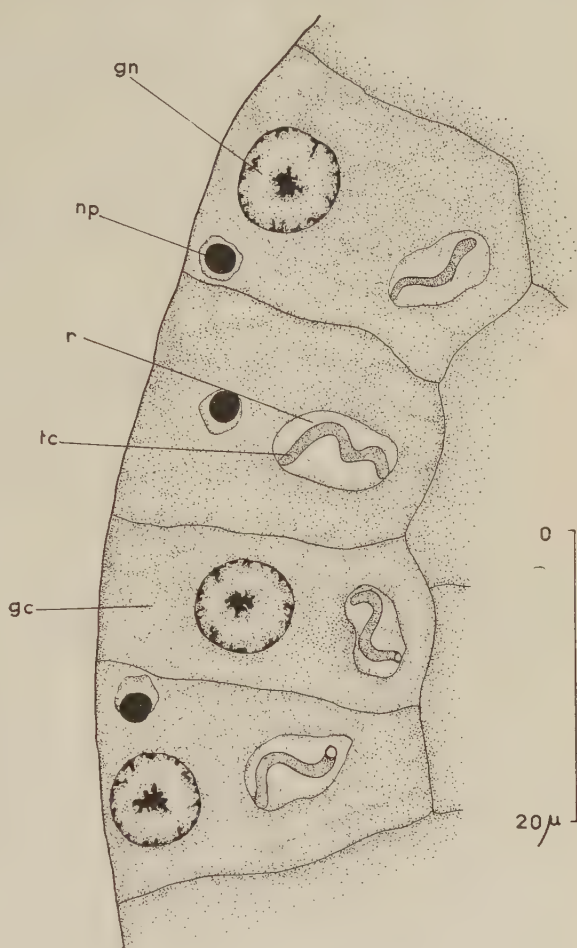

Fig. 9. — *Larve âgée* (trois jours après la mue) *(Halmi, Hotchkiss-Mac Manus).*

gn, gros noyaux ; *gc*, grandes cellules ; *np*, noyaux intermédiaires en pycnose ; *tc*, terminaison du canalicule ; *r*, réservoir intracellulaire.

dans les deux cas, les mitoses dans la glande mandibulaire n'intéressaient que les petites cellules centrales ; nous n'avons jamais observé de division des grandes cellules sécrétrices.

Les deux catégories de cellules ont donc des fonctions bien différentes : les grandes cellules sont sécrétrices, les petites cellules servent à former leurs canaux évacuateurs, qui apparaissent ainsi comme des formations cuticulaires. Une telle dualité de structure est extrêmement fréquente chez les Arthropodes (Cf. Richards, 1951), et a été décrite récemment par Barth (1955) dans les coussinets tergaux d'un Termite (*Syntermes dirus*) ; on peut peut-être rapprocher ceci de la structure des soies (cellule trichogène et cellule tormogène). Les modifications subies au cours de la mue n'ont été étudiées que dans un petit nombre de cas (Wigglesworth, 1933 ; Kuhn et Piepho, 1938), mais il paraît exister une grande variété dans les phéno- mènes.

III. — VARIATIONS AU COURS DU DÉVELOPPEMENT POST-EMBRYONNAIRE ET DANS LES DIFFÉRENTES CASTES

1º *Anatomie*. — La forme générale de la glande varie très peu. La struc- ture générale est acquise dès l'éclosion et ne change plus par la suite.

2º *Taille de la glande*. — Nous avons mesuré, sur coupes histolo- giques sériées et pour chaque stade et caste, la longueur et la largeur maximum de la glande. Chaque chiffre moyen indiqué dans les tableaux I et II porte sur une vingtaine de glandes (sauf pour le premier stade et les néoténiques d'âge connu).

Compte tenu de la variabilité au sein d'une même caste ou d'un même stade, on peut noter les faits suivants (voir tableaux I et II) :

Comme on pouvait s'y attendre, la taille de la glande augmente régulière- ment au cours du développement larvaire et nymphal (croissance générale de l'individu). Chez les sexués imaginaux fonctionnels, et chez les sexués néoténiques, la taille de la glande est plus élevée que dans les autres castes. Du fait que ces animaux sont nourris par les autres individus, on peut se demander si la glande mandibulaire joue un rôle direct dans la nutrition (salivation par exemple). Notons qu'au moment de l'essaimage, la glande a une taille comparable à celle d'une nymphe du dernier stade. C'est donc postérieurement que la glande prend son développement maximum.

Remarquons surtout le cas des néoténiques. Ces individus, bien que pro- venant de larves plus jeunes que les imagos, acquièrent des glandes mandi- bulaires presque aussi grosses. On ne sait si la glande se développe à la mue ou postérieurement, mais quoi qu'il en soit, la glande mandibulaire a atteint son plein développement dès que le néoténique est fonctionnel (comparaison des néoténiques de 2 mois et 1 an 1/2 au tableau II).

Chez les sexués imaginaux et néoténiques, les chiffres du tableau II indiquent un léger dimorphisme sexuel, mais les différences ne sont sans

doute pas significatives. Chez les soldats, malgré le développement très important de la mandibule, la glande mandibulaire conserve une taille relativement petite. Dans les cas où l'on connaissait le stade d'où était issu le soldat, il semble que la taille de la glande ait peu varié au cours de la transformation.

TABLEAU I   (dimensions en microns)

| Stade ou Caste | Taille de la glande | | | | | Hauteur moyenne des cellules | Diamètre des noyaux |
| | Longueur | | Largeur | | Moyenne | | |
	m	M	m	M			
Larves 1ʳ st.	40	50	45	55	50		6,6
Larves 3ᵉ st.	95	120	125	140	122	22	7,2
Larves 4ᵉ st.	125	140	140	160	138	23	6,8
Larves agées	165	215	180	215	185	24	7,1
Nymphes dernier st.	190	240	195	240	208	25	6,8
Ailés	185	235	190	240	209	24	7
Sexués imaginaux	220	280	240	315	260	27	7,2
Néoténiques	215	260	240	270	238	33	7,1
Soldats blancs	120	155	170	195	163		6,9
Soldats	165	200	190	240	195	20	6,5

3⁰ **Taille des cellules.** — On ne saurait tirer des conclusions définitives des mesures effectuées. Toutefois, il semble qu'au cours du développement larvaire, mis à part les premiers stades, la taille des cellules sécrétrices augmente, mais faiblement. Il est d'ailleurs visible sur coupe que, lorsque la glande est plus grosse, il y a davantage une augmentation du nombre que de la taille des cellules. En revanche, quel que soit l'individu considéré, le diamètre des noyaux des cellules sécrétrices est toujours à peu près de 7 μ. Il y a donc au début du développement larvaire une diminution du rapport nucléoplasmatique, qui se ralentit par la suite.

4º *Discussion.* — Les deux catégories de cellules sont reconnaissables dès l'éclosion, et l'étude du développement post-embryonnaire ne nous renseigne pas sur leur différenciation. La croissance de la glande est le fait à la fois d'une augmentation de taille et du nombre des cellules ; sauf dans les tout premiers stades, la multiplication est plus importante que l'hypertrophie. Nous n'avons jamais observé de division des grandes cellules sécrétrices (p. 173), mais, étant donné la lenteur de la croissance, ceci ne

TABLEAU II (dimensions en microns)

| Caste | Taille de la glande | | | | | Hauteur moyenne des cellules | Diamètre des noyaux |
| | Longueur | | Largeur | | Moyenne | | |
	m	M	m	M			
Sexués imaginaux ♂	240	280	245	270	255	27	7
Sexués imaginaux ♀	210	270	260	300	268	27	7,3
Néoténiques ♂	220	290	215	270	235	30	7
Néoténiques ♀	230	280	240	275	248	31	7,2
Néoténiques 2 mois	235	280	210	260	245	31	7,2
Néoténiques 1 an ½	210	255	225	275	250	32	7,2

prouve rien ; il est possible que les nouvelles cellules sécrétrices proviennent de la différenciation des petites cellules centrales, mais nous n'en avons aucune preuve.

Si la glande mandibulaire varie peu d'une caste à l'autre, il convient pourtant d'insister sur le développement qu'elle subit chez les sexués quand ils acquièrent la maturité génitale. Nous ne savons pas ce que signifie fonctionnellement cette hypertrophie, mais elle s'observe aussi bien chez les imagos que chez les néoténiques. Malgré leur morphologie larvaire et leur développement abrégé, les sexués néoténiques acquièrent donc des caractères histophysiologiques semblables à ceux des imagos fonctionnels ; outre la glande mandibulaire, on peut encore citer : l'hypoderme (Jucci, 1924), les cellules neuro-sécrétrices (Noirot, 1957), la glande sternale (Bregeon, 1959). Si nous ne savons pas encore l'interpréter en termes physiologiques, la convergence de l'évolution structurale mérite d'être soulignée.

Résumé.

La glande mandibulaire de *Calotermes flavicollis* est constituée de deux types distincts de cellules : dès grandes cellules sécrétrices dont chacune déverse son produit de sécrétion à l'extérieur par l'intermédiaire d'un canalicule, et des petites cellules centrales. Au moment de la mue, les canalicules sont rejetés, et les petites cellules élaborent les nouveaux canalicules effectuant une migration centrifuge, puis dégénèrent.

Dès l'éclosion, la glande mandibulaire est différenciée. Au cours du développement post-embryonnaire, elle augmente de taille, sans que son anatomie varie. Entre les différentes castes, les variations sont peu considérables, mais le développement de la glande est maximum chez les sexués fonctionnels, imaginaux et néoténiques.

Summary.

The mandibular gland of *Calotermes flavicollis* consists of two distinct types of cells: large secretory cells each of which pours its secretion to the exterior by means of a small duct, and small central cells.   At moulting time, the ducts are discarded and the small cells form fresh ducts and migrate to the periphery, after which they degenerate.

The mandibular gland is differenciated at the time of hatching.   During post-embryonic development it increases in size without any change in anatomy.   The differences between the castes are of little significance, though the development of the gland is at its maximum among functional reproductives, imagoes or neoteinics.

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SUR LE NID ET LA BIOLOGIE
DE *MACROTERMES GILVUS* HOLMGR.
DANS LES RIZIÈRES DU CAMBODGE

par CH. NOIROT

Au cours d'un très bref séjour au Cambodge en 1956, nous avons pu observer quelques Termites de ce pays. Nous n'avons pu faire qu'une étude sommaire, qui nous a permis néanmoins de poser quelques problèmes.

Le Termite connu sous le nom de *Macrotermes gilvus* est très commun dans le Sud-Est asiatique (Malaisie, Indochine, Java, Bornéo, Célèbes, Philippines), mais le statut de cette belle espèce demande à être précisé. Elle n'est certainement pas à sa place dans le genre *Macrotermes* s. str. (voir Grassé et Noirot, 1951) ; si elle se rapproche morphologiquement des *Bellicositermes* africains, sa biologie est nettement différente. D'autre part, l'espèce *gilvus* paraît assez variable et on a décrit de nombreuses variétés (voir Kemner, 1934 ; Snyder, 1949) ; à tous égards, une révision systématique serait souhaitable.

1º *Description du nid.*

Le nid de cette espèce a été décrit par de nombreux auteurs (voir Kalshoven, 1955), mais les descriptions ne sont pas toujours suffisamment précises ; les travaux les plus sérieux sont ceux de Haviland (1898), Bathellier (1927), Kemner (1934) et surtout de Kalshoven (1936, 1955, 1956 *a* et *b*). Il en ressort que l'architecture de la termitière est assez variable. Les nids que nous avons étudiés occupent un milieu très particulier ; celui des rizières de la plaine du Mékong, presque entièrement inondées pendant la saison des pluies (c'est-à-dire en été). Les dômes construits par *Macrotermes gilvus* sont très abondants ; certains sont désertés par les occupants primitifs, et souvent réoccupés par des *Odontotermes*, mais beaucoup sont habités par des sociétés prospères. Voici la description d'un grand nid que nous avons fouillé près de Kompong-speu (50 km à l'ouest de Phnom-Penh).

La termitière est un monticule en cône irrégulier, haut de 2 m et large de 3,50 m à la base, construit en matériau terreux compact, mais assez friable. Une *muraille*, dont l'épaisseur varie entre 40 et 90 cm, recouvre l'*habitacle* subcentral. La *muraille* extrêmement massive est parcourue de *galeries* très peu nombreuses, mais assez larges (3 à 4 cm), souvent orientées suivant les génératrices du cône, et creusées çà et là de chambres à peu près horizontales, dont le diamètre varie de 8 à 30 cm, et la hauteur de 4 à 10 cm.

Ces chambres contiennent les *meules à champignon* ; les plus petites sont
entièrement remplies par une seule meule ; les plus grandes, souvent irré-
gulières, contiennent parfois 2 ou 3 meules. La densité de ces chambres est
faible au sein de la muraille (fig. 2, pl. I).

L'*habitacle* (fig. 5, pl. II) est en continuité avec la muraille, et il n'existe
aucune trace de paraécie ni d'idiothèque, mais on passe sans transition de la
muraille compacte à l'habitacle alvéolaire. Cet habitacle se présente comme
une grande cavité, haute de 60 cm, dont la largeur maximum (à la base)
est de 75 cm, cloisonnée par des lames d'argile sableuse de 3 à 10 mm
d'épaisseur, à peu près horizontales, réunies les unes aux autres par de fins
piliers verticaux et des lames obliques irrégulières ; l'ensemble est assez
grossier et irrégulier. Sur les cloisons, quelques meules à champignon de
petite taille se voient çà et là, mais au total il y a *très peu* de meules dans
l'habitacle. La *cellule royale* a été trouvée près du sommet de l'habitacle,
au sein d'un gros nodule argileux assez mal individualisé.

Il importe de noter la hauteur de l'habitacle au-dessus du sol : la base
de l'habitacle est en effet située à environ 1 m *au-dessus* du niveau du sol
environnant, et la cellule royale était donc à près de 1,50 m de hauteur.

Un autre nid a été sommairement exploré, sur la route de Kampot,
à 35 km au sud-ouest de Phnom-Penh ; ce nid était situé sur le talus de la
route, route en chaussée surélevée d'environ 1,50 m au-dessus de la rizière.
La termitière était un dôme surbaissé d'environ 0,50 m de hauteur, en
argile bistre clair. La fouille sommaire nous a révélé une structure interne
tout à fait semblable au nid précédemment décrit, avec une muraille
massive contenant des chambres à meules et un habitacle central assez
grossièrement cloisonné, la cellule royale occupant le sommet de cet habi-
tacle. Seule différence importante avec le cas précédent : l'habitacle est en
majeure partie *souterrain*, la cellule royale étant située sensiblement au
niveau du sol. Cette différence peut être en rapport avec l'*âge* des deux nids
étudiés. Alors que le grand nid épigé appartenait certainement à une société
âgée, le petit nid souterrain était occupé par une assez jeune colonie
(longueur de la reine : 42 mm). Mais peut en outre intervenir la situation
de la termitière par rapport à la nappe phréatique : le premier nid était édi-
fié au milieu de la rizière, sur une petite digue en terre, émergeant à peine en
saison des pluies ; le second, au contraire, était situé au sommet du talus de
la route, le sol, à cet endroit, dominant d'environ 1,50 m le niveau des
hautes eaux.

A l'ouverture du nid, les habitants manifestent un comportement de
fuite extrêmement marqué ; les ouvriers s'enfoncent dans les galeries pro-
fondes en emportant le couvain, les soldats, grands et petits, se retirent éga-
lement, mais beaucoup se postent à l'entrée des galeries, ou dans les anfrac-
tuosités des meules à champignons, les mandibules largement ouvertes
dépassant seules de l'orifice.

Notons encore que les grands soldats pénètrent à l'intérieur de la cellule
royale, contrairement à ce qu'on observe chez *Bellicositermes natalensis*.

2° *Comparaison avec les nids d'autres régions.*

La récente mise au point de Kalshoven (1955) nous dispensera de rapporter le détail des observations antérieures. Si la figure donnée par Haviland (1898) pour un nid de Bornéo correspond bien à nos observations, nous constatons d'importantes différences entre les nids du Cambodge et ceux décrits tant dans la région de Saïgon (Bathellier, 1927) qu'à Java (Kemner, 1934 ; Kalshoven, 1955). Notons que Haviland et Bathellier ont étudié (en principe) la même sous-espèce *malayanus*. D'une façon générale, les termitières que nous avons observées sont beaucoup moins étalées en surface que celles précédemment décrites ; les meules à champignons sont pour la plupart disséminées *dans* la muraille, et l'habitacle n'en contient qu'un petit nombre ; l'habitacle lui-même, parfaitement individualisé, n'est pas séparé de la muraille, il n'y a pas trace d'idiothèque ni de paraécie (1), et les cloisons de l'habitacle sont plus grossières. Enfin l'habitacle est unique, contrairement aux nids de Java, qui sont fréquemment polycaliques (conséquence de l'étalement en surface ?).

Il est bien difficile de savoir si les différences sont dues à l'existence de races géographiques ou bien aux variations des conditions écologiques. Les nids que nous avons étudiés vivent dans un milieu très particulier ; dans la rizière, *Macrotermes gilvus* établit ses termitières sur les digues en terre qui séparent les champs de riz ; ces digues sont peu élevées et, quand la rizière est inondée (pendant plusieurs mois en été), elles émergent à peine (10 à 20 cm) ; il est donc impossible aux Termites d'établir des constructions permanentes dans la profondeur du sol ; en revanche, si la société s'installe sur un sol plus élevé par rapport au niveau des hautes eaux, elle peut alors s'épanouir sous la surface du sol, et c'est ce que nous avons effectivement observé dans le cas du deuxième nid étudié ; la surface du sol était à 1,50 m au-dessus du niveau des hautes eaux, et la majeure partie de l'habitacle était souterraine, atteignant une profondeur de 0,40 m à 0,50 m.

Dans les rizières de Java, Kalshoven (1954) a signalé l'abondance des nids de *Macrotermes gilvus*, dans des conditions exactement comparables à celles des rizières du Mékong ; mais il n'a pu en étudier la structure interne ; dans ces régions, *Macrotermes gilvus* construit un nid entièrement épigé, ce qui rejoint nos observations, mais plus étalé en surface.

Il est certain que la grande espèce que constitue *Macrotermes gilvus* a su s'adapter à des conditions écologiques aussi variées que celles de la forêt tropicale et de la rizière périodiquement inondée ; mais nous ne savons pas si ce sont des races différentes qui peuplent ces divers milieux. La pratique habituelle de l'inbreeding chez les Termites favorise évidemment la formation de races locales, et le passage de l'espèce dans les Iles indonésiennes et les Philippines a pu encore accentuer les processus d'isolement.

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(1) L'existence d'une idiothèque et d'une paraécie n'est démontrée que pour les nids de Java (KALSHOVEN, 1955).

3º La survie des Termites pendant les hautes eaux, le rôle des meules à champignons.

Quand la rizière est inondée (c'est-à-dire pendant tout l'été), les Termitières de *Macrotermes gilvus* sont parfois complètement isolées par les eaux et apparaissent alors comme de petites îles (fig. 1 et 3). Même quand l'isolement n'est pas total, la termitière n'est en relation qu'avec les levées de terre délimitant les champs de riz, petites digues étroites, émergeant à peine, et ne portant qu'une végétation clairsemée. Comment peut se nourrir l'abondante population du nid, alors qu'elle n'a accès qu'à une quantité de matière végétale extrêmement réduite, bien insuffisante pour couvrir ses besoins ?

Divers auteurs ont mentionné la présence d'amas de débris végétaux dans les parties inférieures du nid, comparables aux « amas de sciure » de *Bellicositermes natalensis* ou aux « amas de rondelles de feuilles » des *Macrotermes* africains. Les observations les plus précises sont celles de Kalshoven (1956), dans le travail duquel on trouvera en outre la bibliographie de la question. Nous n'avons pas observé de telles réserves dans nos fouilles, simplement peut-être parce que le temps nous a manqué pour creuser assez en profondeur, mais il ressort des observations antérieures que ces débris végétaux ne sont pas présents dans tous les nids, et que les quantités entreposées sont très faibles (quelques dizaines de grammes tout au plus) ; il ne peut s'agir de véritables réserves, et nous souscrivons volontiers à l'opinion de Kalshoven, qui y voit plutôt un dépôt temporaire entre la récolte et l'incorporation de ces matériaux aux meules à champignons.

Ce sont bien plutôt les meules à champignons elles-mêmes qui nous paraissent constituer les véritables réserves alimentaires de la Société.

Nous avons déjà montré (Grassé et Noirot, 1957, 1958) que les meules à champignons constituent un aliment normal et important de la société chez les Macrotermitinæ.

La meule à champignons de *Macrotermes gilvus* est formée de lames contournées, à peu près verticales, d'une épaisseur voisine de 1,5 mm, irrégulièrement soudées les unes aux autres ; lorsque les soudures sont nombreuses, elles délimitent des alvéoles verticaux grossièrement en nid d'abeille, mais souvent les lames restent bien distinctes, laissant alors entre elles de larges fentes. L'évolution de cette meule paraît très régulière et tout à fait comparable à celle des *Macrotermes s. str.* d'Afrique ou des éléments de meules de *Protermes* : accroissement par dépôt de matériaux frais sur la partie supérieure des lames, consommation des parties anciennes, c'est-à-dire de la tranche inférieure desdites lames.

Dans les deux Termitières de *Macrotermes gilvus* que nous avons fouillées, et dans un troisième nid très rapidement examiné, les traces de consommation des meules sont particulièrement visibles (pl. II, fig. 4 et 6), la face inférieure de la meule est évidée en sa partie centrale, et les lamelles contournées qui constituent l'édifice montrent dans cette zone une section

fraîchement érodée, où le « velours » mycélien n'a pas le temps de repousser ; la consommation doit être importante et rapide, car toutes les meules présentent cet aspect. En revanche, les apports récents sur la partie supérieure des lamelles (facilement reconnaissables à leur couleur plus foncée) sont peu abondants : un grand nombre de meules en sont complètement dépourvues, et, quand les apports sont visibles, ils n'intéressent le plus souvent qu'un secteur de la meule. Ces observations ont été faites le 21 et le 28 juin, c'est-à-dire peu de temps après l'inondation de la rizière. Ces sociétés étaient donc réduites depuis peu à un approvisionnement extérieur déficient, d'où la faible importance des apports récents sur les meules à champignons. Nous pensons que, pendant toute la période des hautes eaux, il en est de même : les Termites se nourrissent aux dépens des meules à champignons (ce qui paraît être un phénomène normal dans toute la sous-famille des Macrotermitinæ), mais ne peuvent pas, pendant cette période, compenser cette consommation par des apports équivalents de matériaux frais, leur aire de récolte étant extrêmement réduite par l'inondation. Ainsi, outre leur rôle symbiotique général, les meules à champignons constitueraient ici des réserves alimentaires, permettant aux puissantes sociétés de *Macrotermes gilvus* de traverser les conditions trophiques très défavorables de la saison des pluies en zone inondée.

Des observations faites à différentes périodes de l'année devraient assez facilement permettre de savoir si notre hypothèse est exacte.

4⁰ *La fructification des champignons.*

Il est possible que les faits soient plus compliqués, car nous n'avons pas tenu compte de la fructification possible des *Termitomyces*. Au Cambodge et au Viet-Nam, comme le signalait déjà Bathellier en 1927, les « champignons des Termitières » sont bien connus des habitants, qui les récoltent et vont les vendre au marché. La poussée des carpophores paraît se faire au début de la saison des pluies ; Bathellier signale le mois d'août en Cochinchine ; dans les environs de Phnom-Penh, on m'a indiqué plutôt le mois de juillet et même la fin du mois de juin. Mais de quelles termitières proviennent ces champignons ? Plusieurs espèces interviennent très probablement. Bathellier a pu étudier les phénomènes chez *Odontotermes horni* où il paraît fréquent, mais n'a pu en saisir que quelques phases chez *Macrotermes gilvus*, et seulement dans un nid abandonné par ses habitants. Certes, les Cambodgiens vont chercher les champignons sur les grands monticules, œuvres de *Macrotermes gilvus*, mais ceux-là sont fréquemment occupés secondairement par divers *Odontotermes*.

Dans un grand nid examiné très superficiellement le 28 juin, nous avons observé le début de la poussée d'un carpophore sur plusieurs meules, le stade le plus évolué montrait un gros cordon blanchâtre, dressé, long de 15 mm et large de 4, se terminant au sommet en une pointe arrondie ; la meule elle-même avait à cela près un aspect normal avec partie inférieure

rongée; la termitière en question paraissait prospère. Une telle évolution du *Termitomyces* n'a été constatée dans aucune des meules des deux nids que nous avons fouillés plus complètement.

Au total, nous ne savons pas si la fructification des *Termitomyces* est ou non un phénomène fréquent chez *Macrotermes gilvus*, et si ce phénomène peut jouer un rôle notable dans le bilan alimentaire de la société.

Résumé.

Macrotermes gilvus est fréquent dans les rizières de la plaine du Mékong, inondées plusieurs mois chaque année. L'architecture des nids est décrite et comparée à celle d'autres régions.

Le problème de l'alimentation des Termites pendant les hautes eaux est examiné ; il semble que les meules à champignons jouent le rôle de réserves alimentaires, permettant la survie des sociétés.

Summary.

Macrotermes gilvus is common in the paddy-fields of the Mekong plain which are inondated for several months of the year. The architecture of the nests is described and compared with that of nests from the other regions.

The problem of the food supply of these Termites during floods is examined. The fungus gardens appear to be food reserves that enable the survival of the colonies.

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LÉGENDES DES PLANCHES HORS TEXTE

Planche I.

Fig. 1. — Grande termitière de *Macrotermes gilvus* au milieu de la rizière inondée. Près de la route de Kampot, à 25 km de Phnom-Penh, 26 juin 1956.

Fig. 2. — Début de l'ouverture d'un grand nid, près de Kompong-speu, dans la rizière (le plan d'eau est visible à gauche). La coupe passe seulement dans la muraille, très massive, creusée de quelques galeries et de chambres contenant les meules à champignons.

Planche II.

Fig. 3. — Vue de la rizière prise de la route allant de Phnom-Penh à Kampot, le 26 juin 1956, montrant une termitière complètement isolée par les eaux.

Fig. 4 et 6. — Deux meules à champignons vues par leur face inférieure (4) et par leur face supérieure (6). La partie inférieure est nettement évidée en son centre ; sur la partie supérieure de la plus petite des meules, des apports récents sont visibles, mais n'intéressent pas toute la surface, mais seulement la moitié située en bas de la photographie.

Fig. 5. — Coupe verticale dans l'habitacle du nid de la figure 2, planche I ; cet habitacle est nettement distinct de la muraille qui l'entoure, mais ses cloisons sont en continuité avec la muraille (pas trace d'idiothèque ni de paraécie). Quelques petites meules à champignons se voient çà et là ; on remarque une lame d'argile oblique permettant une communication rapide entre les étages superposés.

Macrotermes gilvus

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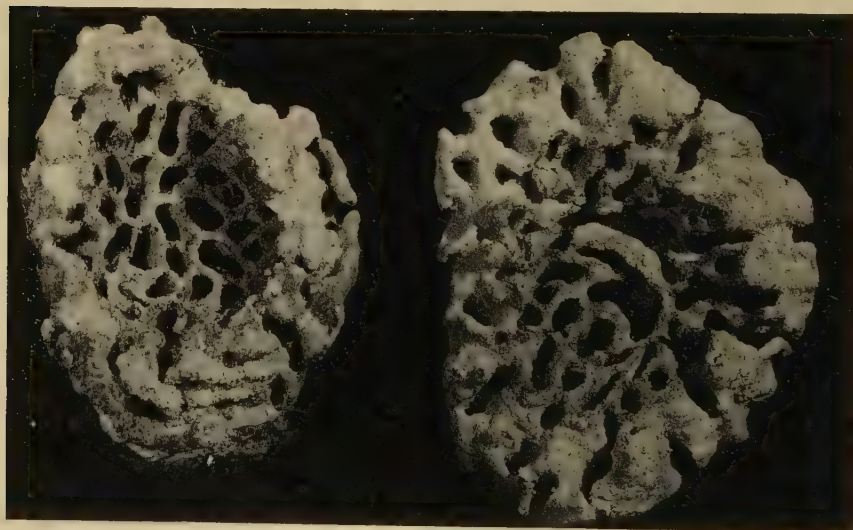
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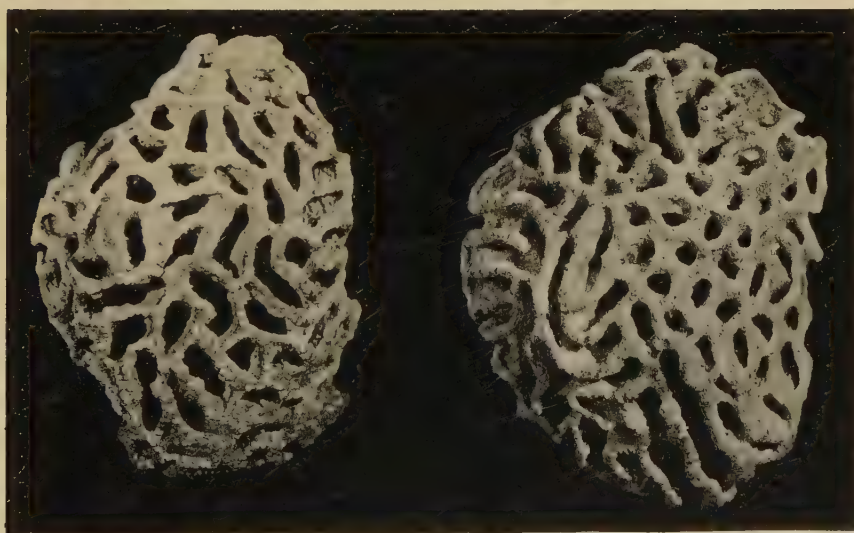
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EGG MASSES AND EARLY LARVAL GROWTH IN *MYRMICA*

by J. S. WEIR

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Introduction.

Experiments described in this paper were carried out in the Zoology Department at Glasgow University during the years 1951-1954. The ants used were collected in the West of Scotland and belonged to the species *Myrmica rubra* L., as subdivided by Brian and Brian (1949, 1955) into *M. rubra macrogyna* and *M. rubra microgyna*. *M. rubra microgyna* was used throughout except where otherwise stated. The laboratory culture methods used have been described by Brian (1951 *b*).

Brian (1951 *a*, 1954, 1955 *a*, 1955 *b*, 1956) has described variations in the development of female larvae. Briefly it has been shown that female larvae may undergo metamorphosis in the summer of the year in which they hatch from the egg and become workers (development via non-dormancy) or may be overwintered and undergo metamorphosis in the following year (development after dormancy). These latter larvae may metamorphose to either workers or queens. The present paper describes experiments designed to investigate the growth of young larvae in the egg mass, and larval development via dormancy or non-dormancy. The conditions necessary for the formation of an egg mass in experimental colony fragments of *Myrmica* have been described elsewhere (Weir, 1958 *c*, 1959 *a*). It has been shown that there is no blastogenic determination of larvae for non-dormancy or dormancy. The present experiments deal with established egg masses and assume developmental plasticity of queen-laid eggs.

THE EGG MASS

Laboratory observations show that the egg mass must be continuously tended by workers during the period prior to egg eclosion. Neglect of the egg mass by the workers results in the loss of the hydrophobic quality of the egg cuticle. The individual eggs lose coherency and the egg mass gradually 'collapses'. Eggs in this condition are often 'licked' by workers before replacement in an egg mass and their surface then becomes hydrophobic again. In large egg masses (three or four hundred eggs) workers usually leave gaps which give them access with their antennae to most regions of the egg mass.

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Brian (1951a, 1953a) and Weir (1958b, 1958c, 1959a) investigated worker oviposition and worker egg eating.

Workers were reared in laboratory cultures on food containing vital dyes (nile blue sulphate, neutral red, waxolene red O.S.). These workers laid coloured eggs. In synthetic colony fragments including such workers, worker-laid eggs were seen to accumulate round a core of earlier queen-laid eggs. (Queen oviposition may begin seven to ten days before worker oviposition.) In other colonies, worker eggs accumulated in separate regions of the egg mass. The possibility therefore appears that workers may be able to differentiate queen-laid eggs from worker-laid eggs. In very many experimental colonies, however, no egg segregation was detected. The way in which the workers disrupt the egg mass was noted in four colonies. They contained egg masses with central cores of queen-laid eggs surrounded by an uneven layer of mixed queen and worker eggs. In two cases, the egg mass was disrupted immediately after observation began, probably due to excessive and abnormal light stimulation. Workers seized portions of the egg mass, tore them from the main bulk, and carried them off. Later, when these fragments were put back by the workers, there did not appear to be any systematic structure in the reconstituted mass. In the remaining two cases, however, workers only broke up the egg mass after larval eclosion. Second instar larvae were present. Though larval flexing movements may have caused some disturbance, they were not directly responsible for the breaking up of the pile which was done by the workers. Larvae were collected, laid on their backs, and some of the eggs remaining placed on or near them.

Two egg masses were examined immediately the first larval eclosion was observed, and those eggs which showed recognisable signs of development were separated from those which did not. There were 255 eggs in the first egg mass of which 130 showed development and 125 did not, while in the second there were 124 eggs of which 72 showed development and 52 did not. Thus when eclosion began in these egg masses from laboratory colonies (comparable to small natural nests), there were approximately equal numbers of *developing* and *undeveloped* eggs in the mass. Observations on a number of other egg masses confirm this.

EARLY GROWTH AND SURVIVAL OF LARVAE

Measurement of the head capsule of larvae showed that three instars are recognisable.

First instar larvae are recognised by the possession of, at most, two hairs (these are always on the head.) The points of origin of other hairs are sometimes visible as cuticular thickenings on the thoracic and abdominal segments, but these are not elongated to form hairs. Second instar larvae show a total of between six and thirty-four cephalic, thoracic and abdominal hairs. Third instar larvae possess a very large number of

hairs (often over two hundred) with considerable individual variation in their length, number, and distribution.

First instar larvae may be divided into two categories (designated IA and IB), characterised as follows:

IA: Length 0,625 — 0.688 mm. No air in tracheae. Head large compared with the body. Visible segmentation. Abdominal segments, tapering in dorsal view.

IB: Length 0.75 — 1.375 mm. Air in tracheae and tracheoles. Body proportions closer to those of older larvae. External segmentation of abdomen difficult to see. Abdomen untapered, rounded.

IA larvae are newly-eclosed larvae and observation shows that the consumption by the newly eclosed larva of one egg can convert the IA larva to a IB larva. IB larvae appear capable of consuming a large number of eggs. IA larvae appear to feed automatically after most types of stimulation. Touching them causes opening and closing of the mandibles, flexing movements of the body, and the initiation of pharyngeal sucking. Normally this would result in the consumption of adjacent eggs in the egg mass since the mandibles of a first instar larva are lightly sclerotised. Experiment shows that first instar larvae are capable of piercing and eating other eggs at any stage of development, although some may be eaten more easily than others.

Experiment 1.—The possible necessity of eggs for the survival of IA larvae was examined in this experiment. Sixty-four of these larvae were cultured in sixteen groups of four, each group with ten vernal* *Myrmica rubra microgyna* workers for eight days at 25ºC. To eight of the cultures ten worker-laid eggs were added, eight cultures received no eggs. The experiment was undertaken in four blocks. Larval survival and egg recovery after eight days are shown in table 1 (A and B) as the total from each block.

TABLE I. — A. LARVAL SURVIVAL IN EXPERIMENT 1.

	WITH TEN WORKER EGGS PER CULTURE.	WITHOUT EGGS.
Blocks 1 + 2	9/16	1/16
Blocks 3 + 4	7/16	1/16

B. EGG RECOVERY IN EXPERIMENT 1.

	WITH TEN WORKER EGGS PER CULTURE.	WITHOUT EGGS.
Blocks 1 + 2	30/40	—
Blocks 3 + 4	18/40	1

(*) The terms pre-vernal, vernal, aestival, and serotinal have been used by Brian (1954) and Weir (1 958 *a*) to describe seasonal changes of worker "condition". They correspond to worker condition in the field during March, May, July, and September, respectively, or to worker condition in the laboratory at 25ºC after 2 weeks', after 5 weeks', after 8 weeks', and after 11 weeks' culture respectively.

Eggs are necessary for significant larval survival, and a significant proportion of the eggs is eaten (either by larvae or by workers).

Two possible explanations of the result of experiment 1 are:

1. The use of eggs as the sole larval food during the first instar. IA larvae have not been observed receiving food from workers; they appear to be completely dependent on eggs.
2. The necessity for a significant bulk of brood before detection or 'recognition' of larvae by workers. Neglect by workers (under the experimental conditions used here), rapidly caused the death of first instar larvae.

Experiment 2.—This experiment was designed to investigate the relative mortalities, under adverse conditions, of first instar and third instar larvae. Twelve cultures, each comprising ten serotinal workers and thirty larvae, were incubated; six at 25°C and six at 20°C. Larvae in three of the cultures at each temperature were of type IB and were cultured with thirty queen eggs (recently laid), while larvae in other cultures were small serotinal third instar larvae. No eggs were included in the latter six cultures. The thirty eggs were added to give an approximately equal bulk of brood, or potential brood in all cultures. Oviposition by serotinal workers is low and can be neglected here (Brian, 1953*a*; Weir, 1958*b*, 1959*a*). Larval survival after fourteen days is shown in table II. Larval

TABLE II. — LARVAL SURVIVAL IN EXPERIMENT 2.

TEMPERATURE.	3RD INSTAR LARVAE. Culture			1ST INSTAR LARVAE. Culture		
	A	B	C	A	B	C
25°C	9	15	11	0	4	1
20°C	16	17	14	12	8	8

mortality with these worker/larva ratios and serotinal workers is heavy. Extreme larval mortality occurs among first instar larvae at 25°C, reared by serotinal workers. Third instar larvae, however, show moderate survival capacity (40 %) under these conditions. High larval mortality is not confined to *Myrmica*. Peacock, Smith, Hall and Baxter (1954) working on *Monomorium* consider that only 25 % of young larvae become adults.

Experiment 3.—This experiment was designed to investigate the effect of other brood forms on larval survival. It comprised fifteen cultures each containing twenty first instar (IB) larvae and twenty aestival workers all cultured at 25°C. Individual cultures contained:- small, overwintered, third instar larvae, of the same nest; or, worker pupae from the dormant brood of the same nest; or, worker prepupae from the dormant brood of the same nest. The number of these brood forms present was varied

systematically. There were three control cultures which contained only the first instar larvae. The survival of first instar larvae in all cultures after fourteen days is shown in table III.

TABLE III. — SURVIVAL OF FIRST INSTAR LARVAE IN EXPERIMENT 3.
Larval survival in the three control cultures was:— 0, 0, 1.

NUMBER OF OTHER BROOD FORMS PRESENT.	OTHER FORMS OF BROOD PRESENT IN CULTURES.		
	Overwintered 3rd instar larvae.	Prepupae from overwintered larvae.	Pupae from overwintered larvae.
2	—	5	—
5	1	3	1
10	1	4	3
25	2	5	5

The results of experiment 3 are inconclusive. They show that, under laboratory conditions, there is a significant difference in the survival of young larvae between cultures containing prepupae and those containing third instar larvae. In several cases young larvae have been observed on the ventral thoracic surface of prepupae. [The placing of eggs on the ventral thoracic surface of the larva is a form of worker behaviour associated with the feeding of larvae. Early third instar larvae in some conditions have a ventral thoracic depression into which eggs may fit so securely that they have to be prised loose with a needle. This forms an interesting comparison with the trophothylax of certain sub-tropical pseudomyrmine larvae (Wheeler, 1928).]

Experiment 4.—This experiment was designed to investigate the effect of callows (recently emerged workers, often observed on top of the brood mass) on the survival and growth of first instar larvae as compared with the effect of aestival, overwintered workers. It comprised eight cultures (each containing twenty workers, and thirty second instar larvae) which were reared for fourteen days, four at 20°C and four at 25°C. Larval survival after this experiment is shown in table IV, and the average length of larvae in table V.

TABLE IV. — LARVAL SURVIVAL IN EXPERIMENT 4.

	25°C		20°C	
Aestival Overwintered Workers	18/30	14/30	25/30	29/30
Callows (three weeks old)	18/30	12/30	7/30	16/30

TABLE V. — AVERAGE LENGTH OF LARVAE IN EXPERIMENT 4.

(1 unit = 0.0625 mm.)

	25ºC		20ºC	
Aestival	34.2	31.2	24.4	23.7
Overwintered Workers				
Callows	32.6	34.0	25.1	22.1
(three weeks old)				

Results show that at 25ºC the survival capacity of the larvae with both worker types is very similar. At 20ºC, however, the survival capacity of the larvae with overwintered aestival workers is much higher than with callow workers. Results of larval growth measurement show that larvae with both types of worker grow faster at 25º C.

Experiment 5.—This experiment investigates larval development in groups. Brian's observations (1951a) show that certain larvae produced from the spring egg peak become dormant, along with most larvae from the summer egg peak. The differentiation of larval development in groups of varying sizes has been repeatedly investigated. Experiment 5 describes such larval developmental divergence in one group of 20 first instar larvae, 20 vernal workers, and 4 prepupae. This is compared with larval development in 10 groups each composed of 2 first instar larvae, 3 workers, and 2 prepupae, all groups being cultured at 25º C. The unequal worker/larva ratio is unavoidable if the effects of worker depression noted by Brian (1953b) are to be avoided. The results of this experiment are shown in figures 1 and 2. In figure 1, the large increase in size shown by certain larvae between the 10th and 14th days indicates that these larvae are potentially non-dormant and will metamorphose during the current season. Three of them did in fact metamorphose. Within the same period of time in which the non-dormant larvae of the large group metamorphose, it is apparent from figure 2 that no larvae in the small colony fragments become non-dormant, in spite of the higher worker/larva ratio in these small cultures. The length of the larvae within each small group remains very similar throughout the experiment, but there is wide variation in the average larval size between all the small groups at any one census. The overall size variation shown by larvae within these small groups produces a larval size range comparable to that shown by the large culture, if the non-dormant brood are discounted. From such differences in the growth of dormant larvae, it is apparent that either inherently 'good and bad' worker groups or inherently 'good and bad' larval groups must exist among individuals of the same age (Weir, 1958a).

While over two hundred larvae have been individually examined and over two hundred reared individually or in groups of two larvae, no non-dormant larvae have been reared from the first instar either in isolation or in groups of two larvae. Certain isolated larvae have metamorphosed

during the same year in which they hatched, but these have either shown
critical developmental differences compared with the non-dormant larvae
produced in groups as described above, or they have been isolated in the
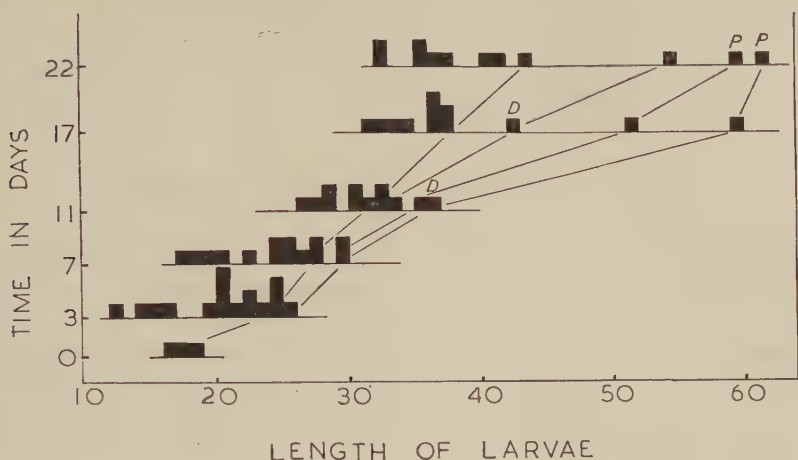

FIG. 1. — Shows the growth of larvae in an initial group of twenty individuals, as a series of size
distributions. The lines indicate probable continuity in the series.
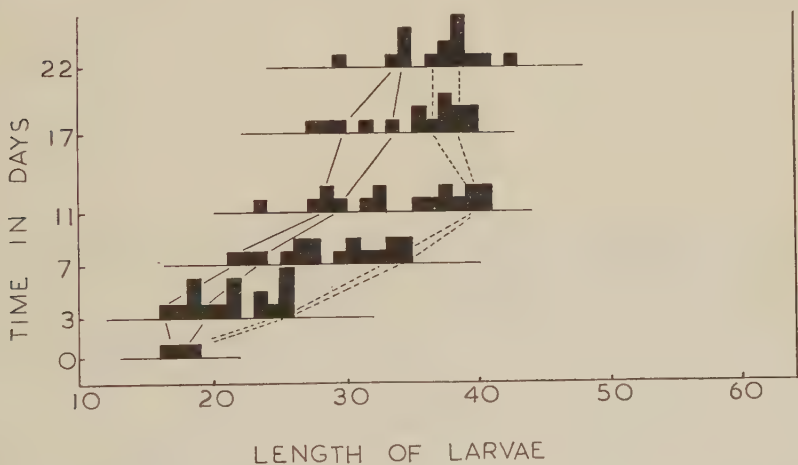
'D'=developing larvae (non-dormant larvae); 'p'=prepupae.

FIG. 2. — Shows the growth of larvae in initial groups of two individuals. The lines indicate
the growth of two typical pairs of larvae. None of these larvae became prepupae.

third instar. These differences will be described elsewhere. The worker/
larva ratios used for these experiments have never greatly exceeded those
ratios known to prevail in nature (Brian, 1953b).

Conclusions from experiment 5 and from similar observations during the
laboratory production of large numbers of non-dormant larvae show that
under these laboratory conditions:

1. Non-dormant larvae occur in larval groups.
2. The range of weights of dormant larvae at dormancy differ. The differences can be attributed to:
   (a) Quantitative effects such as biased feeding in larval groups (Weir, 1958b; Brian, 1956b, 1957).
   (b) Qualitative effects such as differences in worker or larval efficiency (Weir, 1958a, 1958b; Brian, 1956).

THE GROWTH OF LARVAE IN GROUPS

Quantitative effects controlling the production of non-dormant larvae in larval groups were further investigated in experiment 6.

Experiment 6.—This comprised fifteen cultures in three series of five cultures containing different numbers of aestival workers and larvae. The five cultures in each series contained 5, 10, 15, 35 and 75 first and second instar larvae, along with 5, 10, 15, 35 and 75 eggs respectively.

TABLE VI. — PERCENTAGE SURVIVAL OF LARVAE FROM INITIAL BROOD MASS IN EXPERIMENT, 6, AFTER THIRTY DAYS.

LARVAL NUMBER.	WORKER NUMBER.		
	10	25	50
5	100 %	100 %	80 %
10	60 %	80 %	100 %
15	40 %	100 %	100 %
35	22.8 %	31.4 %	42.8 %
75	22.6 %	25.3 %	30.6 %

Cultures in each of the three series contained 10, 25 and 50 workers respectively. The experiment was carried out at 25° C. The individual cultures were in glass basins with smaller basins containing sugar and *Drosophila* larvae. There appeared to be ample food available throughout the experiment. In certain cultures, the brood was heaped by the workers. This may interfere with worker efficiency.

Whereas Brian (1953b) investigated changes in the brood rearing efficiency of workers by variation of the worker/larva ratio while the size of the brood mass was initially constant, in this experiment both the worker/larva ratio and the initial size of the brood mass are varied.

Table VI shows the percentage of brood which survived

This percentage decreases with increasing size of the brood mass and increases with increasing worker number, so confirming in part the observations of Brian (1953b) for cases where there is adjustment by the workers of the size of the brood mass to worker number.

The percentage survival of larvae after thirty days is consistent in cultures of the same worker/larva ratio, irrespective of group size.

The rate of production of pupae and prepupae varies. Table VII shows

TABLE VII. — PUPAE AND PREPUPAE PRODUCED AFTER FOURTEEN DAYS IN EXPERI-
MENT 6.

INITIAL LARVAL NUMBER.	WORKER NUMBER.		
	10	25	50
5	1	2	—
10	1	4	3
15	2	4	6
35	1	5	5
75	3	5	6

the numbers of pupae and prepupae present after fourteen days. In Table VIII these numbers are shown as a percentage of the total number of pupae and prepupae produced in thirty days.

Distributional anomalies in table VIII may be attributed to variation

TABLE VIII. — NUMBER OF PUPAE AND PREPUPAE PRODUCED DURING FOURTEEN DAYS AS A PERCENTAGE OF THE TOTAL NUMBER PRODUCED DURING THIRTY DAYS IN EXPERIMENT 6.

LARVAL NUMBER.	WORKER NUMBER.		
	10	25	50
5	25 %	66 %	0 %
10	50 %	80 %	37 %
15	40 %	40 %	85 %
35	25 %	71 %	71 %
75	27 %	45 %	50 %

in the sizes of pupae and prepupae produced, e.g. the low values in those cultures containing 50 workers and 5 or 10 larvae, similarly with the culture of 25 workers and 15 larvae where large pupae were produced. Unfortunately these data are incomplete. However, it is apparent that the initial size of the larval brood mass may affect the rate of production of pupae and prepupae. In experiments carried out since this work was completed, Brian (1956b, 1957) has noted that nest design and larval size distribution may affect worker efficiency, in rearing of post-dormant larvae. His results are compatible with those described here.

Examination of the total number of non-dormant brood produced during 30 days shows that, if expressed as a percentage of the brood numbers at 14 days (i.e. as a percentage of the numbers of larvae resulting from numerical adjustment by the workers), they decrease both with increased worker number and with increased brood mass size (table IX). Similar figures relative to the initial size of the brood mass show even greater decreases with the above factors. The effects are therefore caused by factors which operate throughout the experiment.

The success of workers in brood rearing in experiment 6 in respect of

TABLE IX. — EXPERIMENT 6.

Column A: The numbers of larvae in the brood mass after being subjected to worker adjustment for 14 days.

Column B: The total number of non-dormant brood produced during the 30 days of the experiment as a percentage of A.

LARVAL NUMBERS.	10 WORKERS.		25 WORKERS.		50 WORKERS.	
	A	B	A	B	A	B
5	5	100 %	6	100 %	5	80 %
10	7	71 %	8	100 %	14	79 %
15	6	100 %	18	72 %	18	50 %
35	8	87 %	15	53 %	18	61 %
75	19	73 %	26	61 %	34	47 %

dormant larvae is shown in figure 3, where the average size of larvae remaining after 30 days is plotted against the worker/larva ratio. While the complete data show a considerable larval size range, the average size of these residual larvae varies with the absolute size of the brood mass as well as with the worker/larva ratio.
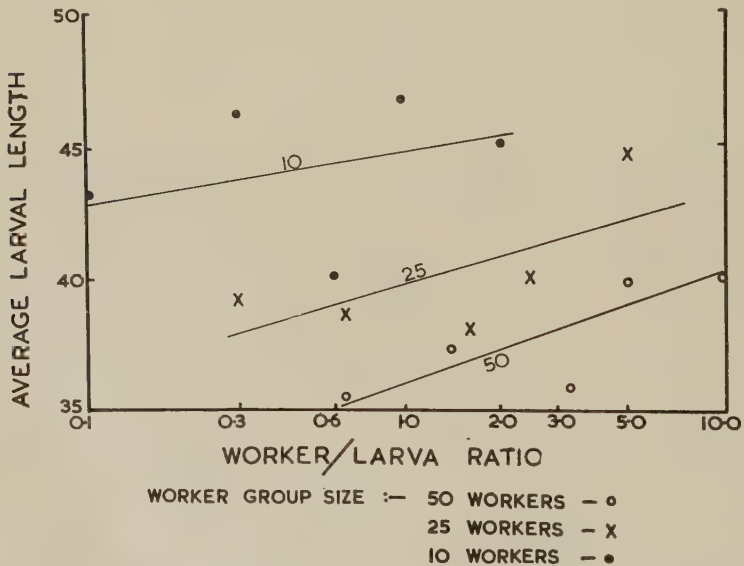
FIG. 3. — Worker brood rearing success after 30 days in experiment 6, in respect of dormant larvae, is shown here. The regression lines have been estimated visually. The third culture in each series shows a striking variation compared with the rest of that series. This is presumably due to an error of experimental technique.

(1 unif of length=0.0625 mms.)

In conclusion, it appears that the success of aestival workers in brood rearing varies with their success in rearing both non-dormant brood and dormant brood (*both* of which were produced), firstly with the worker/larva ratio, and secondly with the absolute size of the brood mass. With increasing size of the brood mass, worker brood rearing was less efficient in respect of larval survival, and the percentage of non-dormant brood produced. Further, with increase of numbers at the same worker/larva ratio, worker brood rearing was less efficient measured by the average size of the residual (dormant) larvae. Such results might be attributable to a shortage of food, yet in all cultures, sugar and *Drosophila* larvae were present. If poor larval brood rearing was caused by food shortage, this shortage was due to worker inefficiency. The only apparent advantages accruing from increased worker numbers were the production of larger prepupae, and, possibly, increased *rate* of production of prepupae and pupae. There is a number of possible explanations of these results. For instance the piling of brood into a heap by workers has been shown to affect subsequent larval growth (Weir, 1958*b*). If the size of the pile of larvae is varied, the number of larvae on the surface (those which are fed and therefore grow) will vary as the surface area of the pile. The problem of biased feeding among piles of larvae has been considered by Brian (1956*b*, 1957). Further, variation in the rate of production of pupae and prepupae can be accounted for by qualitative differences in the food supplied by the workers. The presence of a food material which caused rapid development and was supplied in limited quantity by the workers and in proportion to their numbers would account for this observation.

DISCUSSION

Observation shows that the egg mass is not a colony component which can be neglected by the workers, or by the queen if no workers are present (Weir, 1958*c*, 1959*a*). It has structure, at least inasmuch as gaps are left to give antennal access to the centre of large clumps, and it requires care to prevent gradual disintegration under experimental conditions of high humidity. It has been shown that these experimental nests (Brian, 1951*b*) may be inefficient, first since they do not provide full worker employment in 'preferred' occupations (Weir, 1958*a*, 1958*b*), and secondly in respect of structure and size, as measured by the growth of post-dormant larval groups (Brian, 1956*b*). Therefore they may not be ideal for egg production and egg rearing, and egg masses may require more attention than they would receive in nature. There is no evidence of any consistent structure or systematic organisation of the egg mass in experimental nests, such as would result in the determination of particular eggs, or of eggs from a particular source, for development into dormant or non-dormant larvae. From evidence considered up to this point, such determination must occur at the earliest during the first instar.

Observation has failed to reveal any differentiation of eggs from newly hatched first instar larvae by the workers. Newly hatched first instar larvae are not fed by workers, nor are they removed from the egg mass on hatching. Experiment 1 shows in fact that the newly eclosed larva feeds on adjacent eggs in the brood mass. If isolated, or kept short of eggs, it dies. Death may be due to neglect as well as starvation, since individual eggs scattered through the nest are sometimes not 'recognised' and tended. Yet the same eggs gathered into a group are 'recognised' and tended (Weir, 1958c, 1959a). The first larvae to elicit any detectable 'interest' from workers are large first instar larvae, or, more usually, second instar larvae. These show vigorous flexing movements on being touched by worker antennae, or being moved. Such larval 'test-servicing' (Brian, 1957) results in the workers disrupting the egg mass, spreading it out and separating the older larvae. There is at this time a range in larval size from second instar larvae to newly eclosed first instar larvae, accompanied by eggs. As a result of the spreading out, there is an increased chance of an egg shortage (food shortage) among the newly eclosed larvae. Those few second instar larvae which can now attract worker attention and worker food, therefore gain heavily in weight by comparison with the larger numbers of first instar larvae still 'waiting' for some of the residual eggs to be placed near them or on them, by chance, by the workers. There may be few residual eggs, since, at the time of the first larval eclosion there are approximately equal numbers of developing and undeveloped eggs. Experiment 3 shows that the survival of these isolated first instar larvae may be increased by the presence of other, larger, brood forms, which do not themselves require food, e.g. prepupae. These prepupae act as a 'centre' on which eggs and young larvae are gathered.

It is apparent that worker efficiency throughout is critical. Neglect by workers at any time from the initial aggregation of the eggs to the feeding of the second instar larvae, will result in heavy larval mortality. Certain workers, under certain circumstances, are inefficient. Experiment 2 shows that serotinal workers at high temperatures, and callow workers at low temperatures are both markedly inefficient. Serotinal workers are associated with low temperatures in the field, where observation suggests that in nature, first instar larvae would eventually become very small third instar larvae which would enter hibernation. Callow workers are often associated with high midsummer temperatures when they are found on the brood mass. In both these cases the use of an 'inappropriate' temperature has resulted in a surprising inefficiency. The physiological reasons for this inefficiency are not known.

The growth of larvae in groups shows that non-dormant larvae are, in nature, derived from those larvae which are separated from the brood mass as second instar larvae, and can attract worker attention at once. These larvae retain, in synthetic groups, their initial 'lead' and can soon be visibly differentiated from the others. There is no evidence to suggest that these larvae are enabled to gain their initial 'lead' in the egg mass by

any other than stochastic factors. The possibility of social regulation of the growth and development of these larvae only arises, normally, in the second instar when workers start feeding the larvae. If larvae are biased towards, or determined for, non-dormancy or dormancy, while in the egg mass, it may be expected that such an inefficient stochastic mechanism would be subject to subsequent social regulation via the workers. This problem is examined elsewhere (Weir, 1959b).

Critical effects in respect of larval determination for non-dormancy and dormancy are attributable to group size, e.g. experiment 6 (cf. Brian, 1957, on post-dormant larvae). If large groups are, in general, inefficient, then non-dormancy is to be considered as a concomitant of inefficiency, small groups being efficient inasmuch as larvae which are hibernated may be 'eligible' for queen determination in the spring. The measurement of efficiency is, here, the production of sexuals. Equally, if the large group is basically inefficient, this inefficiency is rectified by the group itself, in an efficient way, namely by the production of more workers (i.e. the diversion of some potential gyne material from this potential developmental course (after vernalisation) to immediate worker development) so ultimately causing the production of a greater percentage of sexuals from the larvae.

Non-dormancy can then be regarded as a form of socially regulated group adjustment leading to increased social efficiency. Further experiments on the growth of non-dormant and dormant larvae have been undertaken and will be reported.

Summary.

1. Larval eclosion and the conditions of growth of young larvae of *Myrmica* have been examined by observation and experiment.
2. No structural organisation of the egg mass has been observed which would cause the growth and development towards either dormancy or non-dormancy, of larvae derived from any particular group of eggs.
3. First instar larvae are not 'distinguished' from eggs by workers.
4. First instar larvae feed on adjacent eggs in the egg mass. At least one egg is eaten to enable the larva to survive, and many more can be eaten if available.
5. Second instar larvae are 'detected' by workers and removed from the egg mass.
6. In a group of larvae those which reach the second instar in advance of the rest gain the advantage of worker attention and feeding, and are directed towards non-dormancy.
7. The brood rearing efficiency of workers varies with seasonal condition and temperature. The presence of brood at other stages of development may affect the survival of young larvae.
8. These results are discussed in relation to colonial efficiency.

Zusammenfassung.

1. Die Brut und die Bedingungen des Wachstums von den jungen Larven der *Myrmica* wurden durch Experimente und Beobachtung untersucht.

2. Es wurde festgestellt, dass keine baumässige Organisation der Eiermasse, von Larven die von irgend einer besonderen Eiergruppe obstammen, die Schlaf oder Wachsamkeit im Wachstum und in der Entwicklung verursachen wurde.

3. Die Larven in ihrer ersten Stadium sind nicht von den Arbeitern zu unterscheiden.

4. Die Larven in ihrer ersten Stadium ernähren sich von den anliegenden Eiern in der Eiermasse. Jede Larve ist zumindest ein Ei um überleben zu können, auch mehrere wenn sie vorhanden sind.

5. Die Larven in ihrer zweiten Stadium werden von den Arbeitern entdeckt und aus der Eiermasse hervorgeholt.

6. In einer Larvengruppe, haben diejenigen die zweite Stadium im Voraus erreichen, den Vorteil dass sie von den Arbeitern gefüttert und auf Wachsamkeit gehalten werden.

7. Die Wirksamkeit der Arbeiter auf die Brut hängt von der Temperatur und Jahreszeit ab. Andere Entwicklungsstufen können das Leben der jungen Larven beeinflussen.

8. Diese Resultate werden in Beziehung der Fortschritte der Kolonie besprochen.

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FLIGHT AND COLONY FOUNDATION IN TWO *CUBITERMES* SPECIES *(ISOPTERA: TERMITIDÆ)*

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Introduction.

Cubitermes is probably the commonest and certainly the most evident genus of the Termitinae in Africa south of the Sahara. Nearly all members of this sub-family feed on soil, and of their biology and economic status comparatively little is known. The two species dealt with here have been identified by the author as *Cubitermes ugandensis* Fuller and *Cubitermes testaceus* Williams. A general study of these two species was made between February 1955 and January 1956, first at Kawanda Research Station, near Kampala, Uganda, and then from November 1955 at the East African Agriculture and Forestry Research Organisation, Kikuyu, Kenya Colony. A part of this period was given to the study of imagos, primarily of *C. ugandensis* but to a limited extent of *C. testaceus* also. This paper deals with the period between flight and the resumption of cryptobiotic life.

Material.

Both species avoid shaded conditions, being found typically in short open grassland and only in the clearings of woodland. They commonly occur together, occasionally even in the same mound. They have been taken in most parts of Uganda above an altitude of c. 1,050 m., excluding the drier north-eastern regions, in Kenya west of the Rift and in north-west Tanganyika. *C. ugandensis* has been taken also from Haut Uélé, Belgian Congo, and *C. testaceus* from Ruanda Urundi.

The material used for this work was taken entirely from swamp border areas near Kawanda Research Station. The countryside there consists of red soil hills and swampy valleys. The hills carry cultivation and tall elephant grass. The swamps carry Papyrus or dense swamp forest and are bordered by short grass pasture with scattered bushes and trees on dark brown soil. Mounds of the two species occur in large numbers on the short grass pasture (fig. 1), avoiding any parts subject to more than occasional inundation, and here and there on the hills wherever they are neither destroyed by cultivation nor shaded by elephant grass.

Methods.

All the work was done in the laboratory with the exception of a few field observations on flight. A total of about 350 alates of *C. ugandensis* and about 70 of *C. testaceus* were used.

Pieces of mound were used for the transport of alates to the laboratory. A piece, roughly cubical with sides of about 20 cms., would be taken from a part of the mound

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where alates were present.   Further alates would be picked up by the tips of the wings, to prevent fluttering, and presented to openings in the mound piece which they would enter readily.   The piece would be opened carefully in the laboratory and as many alates as needed at any one time extracted from it.   Numerous workers were always present and if the piece was kept damp the alates would retain their health and vigour for many days, so far as could be judged, though the required number was always flown within 24 hours.

A chamber with hardboard walls and glass cover, interior dimensions approxi-

Fig. 1. — Mounds of the two species in a swamp border area near Kawanda, with swamp forest in the background.

mately $30 \times 30 \times$ (height) 10 cms., was used for laboratory flights.   Alates were flown in groups of 20 to 30.   Artificial dealation was used in a few cases by the method described below in connection with wing shedding.   Tandem pairs and others were allowed to run into glass tubes and were then transferred to, or allowed to enter, glass plates.   These were of simple design, single chambered with a single cover glass and no special provision for damping, their interior dimensions being $8.75 \times 5 \times 0.25$ cms. They were filled with topsoil of the locality from which the termites were taken, damped to just below saturation level before installation of the imagos.   After installation the plates were kept flat in dark chambers.   The table below summarises the degree of success of the methods as shown by alates selected at random and flown solely for colony foundation.   Production of larvae is taken as the measure of success.

Species.	Alates flown.	Pairs obtained.	Pairs successful.
C. ugandensis	60-70	29	26
C. testaceus	30	11	11

RESULTS AND DISCUSSION

Flight Periods.—That part of eastern Uganda bordering Lake Victoria is an area of high rainfall and no very definite dry season occurs. Generally, however, there is little rain during December, January and February.

Some picture of alate production can be built up from a number of series of both species taken in this area, mainly by W.V. Harris, over several years, together with observations made in 1955 at Kawanda. It appears that in eastern Uganda there is, associated with the cessation of the 'dry' season, a well defined cyclic production of alates of both species commencing early in February and building up through that month. The bulk of *C. ugandensis* alates fly early in March, those of a few colonies as late as April. Alates of *C. testaceus* fly a little later, generally all in April. In 1955 at Kawanda a second less well defined season of *C. ugandensis* alates occurred, production starting in June, a few colonies releasing alates before the end of that month but most in July and August. A few mounds retained alates until October and November. In the case of *C. testaceus* the second 1955 season began with production starting in October, most colonies having many alates by mid November, when work at Kawanda was terminated. Alates present in November presumably fly before the end of the year, probably near the end of that month, or early in December before the onset of drier weather. The October-November season of *C. testaceus* corresponds with the period of 'short rains' in areas within the distribution of both species but subject to less constant rainfall.

Time of Flight.—The disappearance of alates from a total of about 12 *C. ugandensis* mounds was noted at Kawanda on three occasions, in March, June and July. On each occasion it was clear that the alates had flown either during a sunny day or in the night, after heavy rain. There is no record of the natural flight of these termites and no flights were witnessed at Kawanda. No precise information on time of flight was available from local Africans, because the alates are not collected regularly as food. They are, however, eaten by children as and when they appear, and from this it is known at least that one or both species fly in sunny weather. Laboratory work described below indicates that both species must be daytime fliers.

Flight Behaviour.—The more important observations and tests on flight behaviour may be summarised as follows. Alates of both species removed from the mound under the conditions described were negatively phototactic and gregarious. These characteristics were reversed when they used their wings. Alates would make their first flight only if free of contact with other members of the colony and in the presence of light; thereafter they would fly only in the light. The positive phototaxis and

solitary behaviour of the flown alate of *C. ugandensis* was not readily reversed to the condition characteristic of the unflown alate if flight was made impossible by darkness.

When the mound was opened, those alates exposed to the light but still among other members of the colony remained both gregarious and negatively phototactic. They would always remain with a stream or group of termites and escape from the light at the first opportunity. Often a static group of alates would close up and place their heads down and together, their folded wings forming a rosette, remaining thus until disturbed. Alates picked up by the wing tips with forceps, therebye separated from their fellows but unable to use their wings, remained gregarious and negatively phototactic as before, and would readily enter the piece of mound used for transport to the laboratory. On the other hand, an alate would fly within a few seconds if it was forcibly diverted away from a stream of termites or a rosette group, unless it made contact once more with other members of the colony. Likewise an alate tossed aside when the mound was opened, or dropped from forceps, would fly at once. Having flown even only a few cm., or having been allowed to flutter one or more wings while held with forceps, its previous gregarious and photonegative behaviour was completely reversed. Such an alate would no longer enter the piece of mound voluntarily and would emerge at once if forced in. If it flew a short distance and landed among other members of the colony it would pass through and over them as if they did not exist. Once clear of the mound it would fly always towards the sun, unless the sky was overcast.

The following test was carried out in the laboratory, three times with *C. ugandensis* and once with *C. testaceus*, in all cases with the same result. Ten unflown alates were placed in each of two glass topped pill boxes, about 6 cm. in diameter and 2.5 cm. in depth. These were placed in the flight chamber. The alates always remained gregarious and negatively phototactic, and crowded together on the shaded side of the pill box, their wings forming the usual rosette. Removal of the lid made no difference to this behaviour. Then the alates of one pill box were emptied into the chamber, loosely so that contact between them was lost. These would fly at once. The others would remain as before, strong currents of air or flying alates falling among them and emerging again causing only slight and temporary excitement. Then the second group would be emptied out carefully so that they remained in contact with each other. These would always make their way slowly to the shaded part of the chamber and stay bunched up together. Any alate of the group losing contact with the rest would fly within a few seconds, unless it once more made contact with the group. As flying or running imagos of the first group were constantly passing among them and exciting them the group would be gradually reduced in numbers by defection of its members until the last few were scattered and flew.

Alates of both species flying in the chamber in daylight always flew

towards the nearest window, in whatever way the chamber was revolved during flight. When they rested they did so generally at the top of the chamber wall on that side. When they fell into the shaded part of the chamber, on the window side, they would nearly always walk back to the unshaded side before flying again. If the light was excluded all flying stopped at once, to be resumed when the light returned. Using artificial light in this way the more active alates could be made to fly, stop, fly and stop again at intervals of a few seconds.

Further observations were made on flying in connection with light in the case of *C. ugandensis*. One group was flown towards dusk. Flight continued towards the window until a light meter directed towards the window from the top of the chamber gave a reading of only 0.2 candles/square foot, the lowest reading on the scale. During this period flight activity fell off gradually. Thereafter only a few alates made occasional flights in various directions apparently at random until deep dusk, when the meter needle would scarcely move from zero. After all flight had ceased for some minutes, artificial light was switched on and the majority flew at once. Not unexpectedly the alates would fly towards an ultra-violet lamp at a distance giving readings of less than 0.2 c./square foot, but to ordinary yellow electric light only at a distance giving a reading of appreciably more than this figure. A deep red light of comparable intensity elicited no response at any distance and, dimmed by distance to a point where the alates were only just visible, showed that the walking activity of the alates was not noticeably diminished by darkness. During some ten to fifteen minutes observation no return to gregariousness took place.

By use of the ultra-violet lamp it was found that the flight activity of *C. ugandensis* was to some extent correlated with light intensity, as appeared to be the case with the group flown at dusk. When the lamp was brought nearer to the chamber the number of alates flying at any one time and the strength of their flight both increased, until, with the lamp over the chamber less than a metre away, all except a few sick flew strongly and almost continuously against the glass cover. With the withdrawal of the lamp, flight activity fell off accordingly.

How far the pattern summarised at the beginning of this section is followed in natural flights, remains unknown since none was witnessed. Flight and pairing could not take place with absolute normality in the artificial conditions described, if only because of the premature removal of alates from the mound and the restriction of the flight chamber. Nevertheless it is unlikely that the more important aspects of normal behaviour would be lost and successful colony foundation still take place.

There are few accounts of flight among other *Cubitermes* species. Fuller (1915) gives an account of the flight and pairing of *Cubitermes bilobatus* (Haviland) and a related undetermined species, not known to build mounds and therefore probably not a *Cubitermes* sp. His own observations together with Haviland's quoted notes give a picture of elaborate

behaviour in both species, the sexes pairing after a first flight, the male attaching himself to the abdomen of the female who then carries him on a further flight. Nothing resembling this chain of events was observed in the case of the two Uganda *Cubitermes* and this, together with Fuller's description of the great disparity in size between the sexes, suggests strongly that the alates supposedly of *C. bilobatus* were in fact those of one of the many species of other genera that are found in *Cubitermes* mounds. W. V. Harris (unpub.) noted the emergence of alates of an unidentified woodland *Cubitermes* sp. near Kawanda. In this case the alates emerged from a hole in the ground, the hole surrounded by soldiers; in this instance no observations were made on flight.

It is generally held that winged termites are photopositive at or before the time of emergence. Grassé (1942) concluded that positive phototropism and excitation by other castes of the colony were among the most important factors inducing emergence in day flying Kalotermitidae and Rhinotermitidae. In the case of the two Uganda *Cubitermes* spp. the change of behaviour on the first use of the wings from negative phototaxis and gregariousness to the reverse is so marked that despite the artificiality of the conditions it is hard to believe that a similar change does not take place at the same point under natural conditions. Grassé noted that alates of *Reticulitermes lucifugus* were able to return to the nest when external conditions proved unsuitable for flight. Pickens (1934) noted the same for *R. hesperus*; on one occasion the emerged alates turned back and crowded round the exit holes with heads down and wings forming rosettes. This latter behaviour resembles that of the clearly negatively phototactic unflown *Cubitermes* alates described above.

Descriptions of the flights of Kalotermitidae by various authors are of small groups of alates emerging from exit holes only large enough to allow the passage of one at a time. Among higher termites huge numbers of alates are released through exit holes large enough to allow the passage of several at a time. Fuller (op. cit.) describing the emergence of alates of *Odontotermes incertus* remarked that the pressure of alates might be so great that they would form small upright columns, from the apices of which the individuals flew. In descriptions of flights of termites of all groups, mention is generally made of the presence of other castes ringing the exit holes. It seems unlikely therefore that alates of the Rhinotermitidae and Termitidae generally experience such a complete loss of sensory stimulation by other individuals of the colony before flight as did the *Cubitermes* alates flown in the laboratory, with whom such loss was a condition for flight. Loss of contact can scarcely be concerned with flight in the case of *Hospitalitermes diurnus*, whose alates apparently emerge from the nest, group together outside and fly off all more or less at the same moment (report of Warnodihardjo quoted by Kalshoven, 1958). On the other hand the comparative loss of contact on emergence must often be considerable even among the Termitidae, for instance in *Pseudacanthotermes militaris* as described by Silvestri (1914). The building of 'launching platforms'

by certain species of Macrotermitinae has been described (Harris, 1958, et alia).   These might serve towards the separation of emerging alates.

In the case of the two Uganda *Cubitermes* spp., and perhaps in some other day flying termites, it seems probable that negative phototaxis and gregariousness is not reversed before flight, but inhibited by the factors inducing emergence, and that the comparative loss of contact with other members of the colony resulting from emergence enables flight to take place, with the consequent reversal of negative phototaxis and gregariousness.   Ability to return to the nest, if conditions prove unsuitable for flight, would be advantageous in any termite, particularly among higher termites that produce only one or two flights of large size each year.   If external conditions proved unsuitable, hesitation in taking flight would cause crowding near the exit hole.   This would inhibit flight among those emerging.   Probable emergence factors, such as physical conditions at the periphery of the nest and excitation by other castes of the colony, would have ceased to operate on emergence.   This would allow the return of photonegative and gregarious behaviour, and the alates would retire into the nest.

Wing Shedding.—The duration of the flying time, in daylight in the laboratory, varied from a few minutes to several hours between one group and another of each species.   Generally the lapse of time between the wing shedding of the first and of the last fit individual in each group was only a few minutes, but on a few occasions again several hours.

The sexes were present in more or less equal numbers in most groups flown, selection of alates for laboratory flights generally being made at random.   Under these conditions wing shedding, particularly among males, was obviously stimulated by pairing or attempted pairing.   On the other hand there was no dependence on such stimulation at least in the case of *C. ugandensis*.   Several monosexual groups of *C. ugandensis* were flown, one of females and several of males.   Wing shedding proceeded satisfactorily in all these groups.

Wing shedding in *C. ugandensis* did not seem to be affected by the presence or absence of light.   One group was flown at night in artificial light. After several imagos had shed wings the light was turned off and flight among those still winged ceased.   It was then seen, by means of the deep red light described above, that wing shedding was proceeding steadily.

Flown imagos of *C. ugandensis* frequently tried to fly towards the light after their wings had been removed artificially.   These attempts, marked by jumps into the air with the wing stumps beating strongly, were commonly made at intervals for several minutes, during which time the imago clearly lost its positive phototaxis only gradually.   This behaviour demonstrated that the connection between loss of wings and loss of positive phototaxis was not a direct one.   Pickens (op. cit.) noted similar behaviour in *Reticulitermes hesperus* though in that case the alates had shed wings after emergence without flying at all.   In this connection it is worth

remarking that no alate of either *Cubitermes* sp. was seen to shed wings without prior flight; Lüscher (1951) found that at least three minutes of flight was necessary as a preliminary to wing shedding among the several Termitidae he studied, including *Cubitermes glebae*.

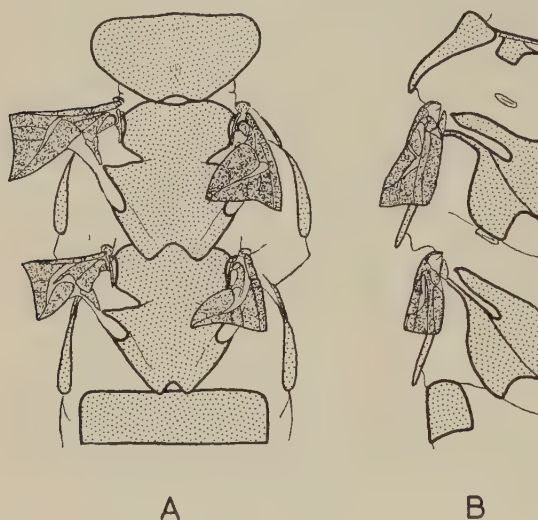The imagos of lower termites have been described by a number of authors as shedding wings one by one, generally with the aid of a rough substrate. Grassé (op. cit.) observed that those of *Kalotermes flavicollis* might also use the abdomen or hind legs for shedding the wings, and considered that torsion was the main mechanical factor involved.

Among Rhinotermitidae and Termitidae the wings are generally shed swiftly, all four more or less together, the method or methods used being obscure, though the abdomen is often involved in pushing up the wings.

The alates of the two *Cubitermes* spp. removed their wings by a movement, sometimes easy, sometimes violent, performed too quickly to be analysed precisely. This movement involved downward arching of the body and raising of the wing blades before they fell away. As a rule the wings were not quite fully flexed at the moment of shedding, but on occasions were fully flexed. Sometimes the hinder part of the abdomen was used to push up the wings. Very rarely the wings were pushed back against the wall of the chamber.

It was found that the most satisfactory method for artificial removal of the wings was as follows. The imago was held by the tips of the wings and allowed to grip a rough surface with its feet. Then each wing would be raised in turn to a near vertical position and a needle run down it to push the stump back towards the horizontal, when the blade would at once come away. The wings would not break away so easily, if at all, if the strain on the suture was applied by torsion or by bending in any other way. For this reason it seems probable that natural shedding is achieved by means of a downward bending strain as described above. This is born out by the observed movements of the imagos and by their morphology. As shown in fig. 2, the basal suture of each wing lies more or less wholly over soft parts of the integument when the wings are not quite fully flexed,

Fig. 2. — Thorax and 1st abdominal tergite of *Cubitermes ugandensis*, the sclerites stippled. (A) Dorsal view, with wing stumps extended on left and flexed on right; (B) Lateral view, with wing stumps flexed.

their usual position at the moment of shedding as described above.   More than half the suture lies over soft parts when the wings are fully flexed. Each wing is supported on one side of the suture by the articulation with the thorax, and on the other side by the stump of the wing behind or by hard sclerites.   If the base of the wing is held down against the thorax by muscular action, downward arching of the body, aided if necessary by upthrust of the hinder part of the abdomen, will raise the blade of the wing and so apply the appropriate bending strain to the suture.

The Calling Attitude.—The calling attitude of these two species is taken up as follows.   The abdomen is raised and arched, so that the terminal part points straight back but is held higher than usual.   The female of *C. ugandensis* walks about very slowly in this position, but that of *C. testaceus* stays quite still.

A female was seldom without contact with a male for more than a minute or two during most of the laboratory flights, due to the overcrowded conditions of the chamber.   Under these circumstances dealate females of both species did not take up the calling attitude until they had run in tandem with, and lost, a male.   They would run about as actively as males until their first run in tandem.   A run in tandem was not a necessary preliminary to the taking up of the attitude at least in the case of *C. ugan-densis*.   When females of *C. ugandensis* were flown in the absence of males, it was found that the dealate females would take up the calling attitude, but only after many minutes of active running.   After a few minutes in the attitude the female would relax, run actively for a few more minutes and then take it up again.   This second pattern may well be common under natural conditions where the imagos would be scattered compared with those in the chamber.   It has been shown above that the imagos do not necessarily shed wings in direct connection with pairing.   A running period before the calling attitude is taken up might, therefore, be advantageous in increasing the chances of successful pairing when the female has shed wings in an area from which males are absent.

In the case of *C. ugandensis* a defense mechanism was noted in connection with vulnerability in the calling attitude.   Occasionally, when approached by a male from behind, a female in the attitude would dart away very swiftly about 5-10 cm., and take up the attitude again.   This reaction could always be elicited with a hair or a needle.   The speed at which the female would move this short distance was greatly in excess of that she could be stimulated to produce when running actively.   This darting reaction seemed clearly designed as a defense against small predators, such as ants, to which the female in the calling position would otherwise be very vulnerable indeed.   The release of this mechanism by males occurred probably only when their approach was not quite conventional.

Tandem Behaviour.—A number of males of both species were attracted to females while still winged.   Some alate females likewise proved attrac-

tive to males, but only a few as the wings generally obstructed the male. Any fit female appeared able to attract any fit male. When the sexes met the male would pass his antennae rapidly down to the hind end of the abdomen of the female, who would at once set off with the male maintaining only antennal contact.

Unattached males were constantly taking the place of those in tandem in the confined space of the chamber. When tandems met the males frequently changed partners. However, when undisturbed either by other males or by difficult obstacles the male-female tandems remained fairly constant. Male tandems were common, particularly when an excess of males were present. When all-male groups were flown, lines of six or more often formed. Male tandems rarely lasted more than a few seconds, and on only one occasion was a male tandem, of *C. testaceus*, constant enough to be mistaken for a male-female one. Female tandems were not seen at all, and no female was ever seen to follow a male.

Females of *C. ugandensis* running in tandem for the first time showed, generally for several minutes, a marked tendency to climb up and down any readily climbable object, such as the walls of the chamber, or matchboxes and books placed in it. Such females would make no effort to find a way round such obstacles or to stay on the chamber floor. This behaviour often resulted in the loss, temporary or permanent, of the following male; possibly this might serve to eliminate unfit males. Subsequently the tandems would remain more on the floor of the chamber but would still frequently climb the walls to the top.

Imagos are described as becoming photonegative and geopositive, after wing shedding, or after pairing, in many of the numerous descriptions of the flight and pairing of day flying termites. Buchli (1950), however, noted that the tandems of *Reticulitermes lucifugus*, whose alates are positively phototactic in flight, wandered about in light or in dark parts of his flight chamber and appeared indifferent to light. In the case of the two *Cubitermes* spp. no reaction towards light, no preference for shaded or unshaded areas, was apparent in any tandem pair or in unpaired dealates, other than those dealated artificially as described above. Tandems of *C. ugandensis* would form and travel about in strong light or darkness with complete indifference. Dealates of both species did not show any obvious tendency towards geotaxis, whether in tandem or solitary. Tandems of subterranean day flying termites, such as these species, would be likely to travel at least a short distance over variably rough terrain before selection of a nest site. The imposition on such tandems of photonegative geopositive behaviour would render this impossible.

Selection of the Nest Site.—Females of both species in tandem would show an interest in gaps under the corner supports of the chamber, or under objects placed in the chamber. This was interpreted as examination of possible nest sites. These examinations would seldom last more than a few seconds and it may be assumed, following Lüscher's studies (op. cit.),

that the absence of moist soil would preclude the use of such places as nest sites.   No test was made on this point but work was done on the thigmo-tactic factor involved.   Semi-circular holes were made in the soil at the edge of the plate under the drawn back cover glass, and it was found that a hole just large enough to accommodate the female was almost always accepted at once.   A hole several times as large would likewise be readily accepted, but one accommodating only about half the female would only be accepted if the female was presented to it several times.

Small depressions and enclosures of one kind or another are innumerable in almost any habitat.   Their use as the start of a burrow would give an obvious defensive advantage against predators.   Skaife (1954) observed that the imago pair of *Amitermes atlanticus* would dig in at the side of a stone or a piece of wood on the ground.   Association of the nest site with wood might be expected in a wood feeding termite, but the use of stones suggests a thigmotactic factor also.   Several authors describe the use of cracks and insect borings in wood by pairs among the lower termites. Thigmotactic behaviour in connection with nest site selection may there-fore be fairly general among termites.

The female would approach to investigate a hole only if the male was following in tandem.   She would enter slowly and curl round to press sideways against the wall of the hole.   After remaining still for some seconds, sometimes half a minute or more, she would either emerge swiftly and walk away with the male in tandem or turn and begin to dig.   Only very great disturbance would cause the pair to leave the nest site once it had been accepted by the female.

Excavation of the Cell.—The female, having accepted a suitable hole and started to dig, would pile the removed soil around the outside of the hole to form a fragile dome over the pair.   The process usually took only about ten minutes as the soil in the plates was loose.   The male might also dig a little when the hole was large enough for him to enter, but the bulk of this initial digging was always done by the female.   Once covered, the pair would become comparatively inactive and would burrow further only very slowly.   The cell would be formed after about two days, and this would be extended only in accordance with the feeding of the imagos and their brood, or in connection with disturbance.   The cells formed in the plates were rather variable in size and shape, but the majority were more or less oval, the width not less than the length of the imagos, that is about 10-11 mm. in the case of *C. ugandensis* and about 7.5-8.5 mm. in the case of *C. testaceus*, and the length about half as much again as the width.

The plates were prepared each with an entry hole for the pair at the middle of one end.   The burrows ran from these holes in a direction generally nearly parallel to the sides of the plate and never approaching the sides closely.   18 pairs of *C. ugandensis* burrowed a mean distance of 3.5 cm. inclusive of the length of the cell, $\sigma = 1.2$.   11 pairs of *C. testaceus* burrowed a mean distance of 3.2 cm., $\sigma = 1.3$.   8 tandem pairs of *C. ugan-*

densis were placed without choice each in a ready-made space, some 2.5 cm. in diameter, in the middle of the plate. All these pairs carved off cells of an appropriate size by means of a wall across the space, without burrowing at all. The direction of the burrows, their similar length in both species although the imagos of *C. ugandensis* are about twice the size of those of *C. testaceus*, and the fact that burrowing in *C. ugandensis* could be eliminated in the way described, suggests strongly that burrowing, as apart from the initial covering of the pair, is dependent on external factors, such as humidity and gaseous exchange, and is not part of a rigid behaviour pattern.

Resumption of Cryptobiotic Life.—The formation of the tandem, with the male acting as a mere appendage of the female, could not be considered as a return to gregariousness in the true sense. Moreover females of both species running in tandem resembled flown alates in treating other imagos merely as obstacles. There was a noticeable slackening of tandem behaviour on the part of the male whenever the female investigated a potential nest site, and tandem behaviour ceased as soon as a nest site was selected. Thereafter the male and female associated in a gregarious worker-like way.

Gregariousness and negative phototaxis are lost together on first use of the wings, and the latter might therefore be supposed to return also with selection of the nest site. The great activity of females when covering the pair after nest site selection, compared with the slow burrowing, does suggest this. However, definite photonegative behaviour was not seen until the pairs were installed in cells.

The Plasticity of Post=flight Behaviour.—It has been explained above, in connection with excavation of the cell, how burrowing was eliminated in the case of 8 pairs of *C. ugandensis*. All these pairs were successful, as measured by production of larvae.

The wings of 3 flown *C. ugandensis* females were removed artificially. Each of these females was placed with a naturally dealate male in a ready-made space in the middle of a glass plate. Each pair carved off a cell without burrowing, as in the case of the 8 pairs mentioned above. Of the 3 pairs, 2 were successful. Thus even the elimination, in the case of the females, of natural wing shedding, tandem behaviour, nest site selection and burrowing did not necessarily prevent colony foundation.

It has been mentioned above, in connection with nest site selection, that females of both species would often emerge from their cells when the cover glasses were removed for cleaning. On these occasions the male would follow in tandem and the female would take up the calling attitude if the male became separated. The female would appear to be once more indifferent to light. Her return to the cell would depend on the thigmotactic factor as for nest site selection. Thus the basis of the run in tandem, selection of the nest site and installation in the cell was repeated,

as many as three times in a few cases, in almost every pair of both species flown solely for colony foundation, with decreasing efficiency for a period of 7-8 weeks in *C. ugandensis* and about 5 weeks in *C. testaceus*, after which females showed no tendency to emerge.

Lüscher (op. cit.) concluded that among the higher termites there was a rigid behaviour pattern concerned with colony foundation, and that interruption of this pattern would be fatal.   In these two *Cubitermes* spp. there does seem to be a rigidity of behaviour concerned with flight, and probably with emergence, but post-flight behaviour is clearly more plastic. A rigid emergence and flight behaviour pattern linked mainly with climatic factors would be most important among termites producing only one or two large flights per year.   Among all termites, however, the post-flight period is characterised above all by imponderables, predation, flooding and so forth.   Ability to take advantage of a particular situation by elimination of one or more of the normal aspects of behaviour, or to repeat a part of the normal behaviour pattern would be of great advantage.

Summary.

Information on flight periods and times of flight of *Cubitermes ugandensis* and of *C. testaceus* in eastern Uganda is reviewed.   All work was done in the laboratory with the exception of a few field observations on flight. Alates removed from the mound were negatively phototactic and gregarious.   These characteristics were reversed by use of the wings. Alates would fly only if free of contact with other termites of the colony and in the presence of light.   Observations were made on the flight activity of *C. ugandensis* in connection with light intensity.   Wing shedding in both species was stimulated by pairing or attempted pairing but, in *C. ugandensis* at least, was not dependent on such stimulation.   Wing shedding was followed by indifference to light.   Artificial wing removal demonstrated that in *C. ugandensis* the connection between loss of wings and loss of positive phototaxis was not a direct one.   The method of wing shedding is discussed.   Females of both spp. did not generally take up the calling attitude until they had paired with, and lost, a male.   In the absence of males, *C. ugandensis* females would run actively for many minutes after wing shedding, after which the calling attitude was taken up between further periods of active running.   An apparent defence mechanism against small predators, used by *C. ugandensis* females in the calling attitude, was noted.   The presence of wings did not inhibit pairing in either species.   Male tandems were frequent but nearly always very inconstant.   Female tandems were not seen and no female was seen to follow a male.   Tandems showed no positive geotaxis and remained indifferent to light.   *C. ugandensis* females tended to climb up and down for some minutes after pairing.   Thigmotaxis proved important in nest site selection by both species.   Burrowing appeared to be dependent

on external factors and not part of a behaviour pattern. Gregariousness returned with selection of the nest site but definite photonegative behaviour was not seen until the pairs were installed in cells. The plasticity of post-flight behaviour is discussed.

Résumé.

Des renseignements sont présentés sur les périodes et les heures de vol de *Cubitermes ugandensis* et *C. testaceus* en Ouganda oriental. Presque tout le travail s'est effectué au laboratoire. Les ailés retirés du monticule étaient grégaires et négativement phototactiques. L'emploi des ailes renversa ces caractères. Les ailés ne volaient que s'ils étaient hors de contact avec d'autres termites de la colonie et dans la lumière. Des observations ont été faites sur l'intensité de la lumière et l'activité de vol chez *C. ugandensis*. La pariade ou un essai de pariade stimula l'amputation des ailes chez les deux espèces, mais, du moins chez *C. ugandensis*, cette stimulation n'était pas obligatoire. Après l'amputation des ailes, les adultes se montraient indifférents à la lumière. Par l'enlèvement artificiel des ailes, on a démontré que le rapport entre la perte des ailes et la perte de la phototaxie positive chez *C. ugandensis* n'est pas direct. Il y a une discussion des moyens utilisé par les adultes pour perdre leurs ailes. En général, chez les deux espèces, les femelles n'adoptaient la posture d'appel que lorsqu'elles s'étaient accouplées avec un mâle et l'avaient perdu. En l'absence des mâles, les femelles de *C. ugandensis* couraient activement pendant plusieurs minutes après l'amputation de leurs ailes, puis prenaient la posture d'appel entre d'autres périodes de déplacement rapide. On nota l'emploi par les femelles de *C. ugandensis* dans la posture d'appel de ce qui paraissait être un mécanisme défensif contre les petits prédateurs. La présence des ailes n'empêcha pas la pariade chez l'une ou l'autre espèce. Des tandems mâles se voyaient souvent, mais ils étaient presque toujours instables. On n'a vu ni de tandems femelles ni une femelle derrière un mâle. Les tandems ne montraient aucune géotaxie positive et restaient indifférents à la lumière. Les femelles de *C. ugandensis* tendaient à grimper et redescendre pendant quelques minutes après la pariade. La thigmotaxie était importante dans le choix de l'emplacement du nid chez les deux espèces. Le creusement paraissait dépendre de facteurs extérieurs et ne pas faire partie d'un schéma de comportement. Une fois l'emplacement du nid choisi, les couples redevenaient grégaires, mais ils ne se montraient absolument photonégatifs que lorsqu'ils s'étaient installés dans des cellules. Il y a une discussion sur la plasticité du comportement après le vol.

Zusammenfassung.

Die Arbeit berichtet über jahreszeitliche und tägliche Flugperioden von *Cubitermes ugandensis* und von *C. testaceus* in Ost-Uganda. Die Untersuchungen wurden fast vollständig im Laboratorium ausgeführt. Geflügelte aus dem Nest genommen waren negativ phototactisch und hielten sich zusammen. Diese Eigenschaften wurden durch den Gebrauch der Flügel ins Gegenteil umgewandelt. Geflügelte flogen nur wenn sie nicht in Gesellschaft mit anderen Termiten des Baues und dem Lichte ausgesetzt waren. Beobachtungen wurden angestellt über Lichtintensität und die Flugfähigkeit von *C. ugandensis*. Abwerfen der Flügel wurde in beiden Arten durch Paarung oder Paarungsversuche gefördert, hing aber, zum mindesten in *C. ugandensis* nicht von solcher Förderung ab. Auf das Abwerfen der Flügel folgte Gleichgültigkeit gegenüber Licht. Künstliche Entfernung der Flügel zeigte, dass bei *C. ugandensis* der Zusammenhang zwischen Flügelverlust und Verlust positives Phototaxis nicht direkt ist. Der Vorgang des Abwerfens der Flugel wird erörtert. Weibchen beider Arten nehmen im allgemeinen keine Lockstellung ein, bevor sie sich mit einem Männchen gepaart und es verloren hatten. Wenn Männchen fehlen, laufen Weibchen von *C. ugandensis* nach Abwerfen der Flügel viele Minuten lebhaft herum, woraufhim zwischen weiteren Perioden lebhaften Laufens die Lockstellung eingenommen wurde. Eine mutmassliche Verteidigungsmethode wenn im Lockstellung von Weibchen des *C. ugandensis* gegen Raubinsekten wurde beobachtet. Das Vorhandensein der Flügel behinderte Paarung in beiden Arten nicht. Männliche Tandems waren häufig, dauerten aber fast nie länger. Weibliche Tandems waren nicht zur Beobachtung, und es wurde nie beobachtet, dass ein Weibchen einem Männchen nachlief. Tandems zeigten keine positives Geotaxis und blieben gleichgültig gegenüber dem Licht. Weibchen von *C. ugandensis* pflegten einige Minuten nach der Paarung auf- und abzuklettern. Thigmotaxis war ein wichtiger Faktor bei beiden Arten in der Wahl eines Platzes für das Nest. Graben scheint von äusseren Faktoren abzuhängen und nicht Teil des Trieblebens zu sein. Der Trieb zur Vergesellschaftung kam mit der Wahl eines Platzes für das Nest wieder, aber deutliche photonegativen Verhalten wurde erst beobachtet, wenn die Paare sich in Zellen eingelebt hatten. Die Plastizität des Verhaltens nach dem Flug wird erörtert.

Literature cited

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NOUVELLES DE L'UNION

DEUTSCHSPRACHIGE SEKTION DER INTERNATIONALEN UNION ZUM STUDIUM DER SOZIALEN INSEKTEN E. V.

ZU UNSERER VOM 9. BIS 12. JULI 1959 IN BERN STATTFINDENDEN

3 TAGUNG

WIRD HIERMIT ERGEBENST EINGELADEN

KARL GÖSSWALD
Für die Sektion

MARTIN LÜSCHER
Für die örtliche Tagungsleitung

Tagungsprogramm

DONNERSTAG, 9. JULI

20.00 Empfang im Restaurant "Innere Enge", Engestrasse 54, durch die örtliche Tagungsleitung den Teilnehmern dargeboten

FREITAG, 10. JULI

8.30 Begrüssungsansprache und Geschäftssitzung
10.30 Erfrischungspause
11.00 12.45 1. Wissenschaftliche Sitzung (Die angegebenen Zeiten schliessen Redezeit und zehn Minuten Diskussionszeit ein).

M. Lindauer, München: Die gegenseitige Verständigung in der Verwandtschaft unserer Honigbiene (11.00—12.15)

F. Köhler, Würzburg: Beitrag zur Analyse des Schwänzeltanzes der Honigbiene durch Auto-Oszillographie (12.15—12.45)
14.30—18.00 2. Wissenschaftliche Sitzung

O. Wahl, Marburg: Stand der Forschungen über den Eiwess- und Vitaminstoffwechsel der Honigbiene (14.30—15.10)

E. Serian-Back, Marburg: Neue Untersuchungsergebnisse über den Vitaminbedarf der Bienen (15.10—15.30)
Gemeinsame Diskussion beider Vorträge (15.30—15.45)

H. Freudenstein, Marburg: Faktoren, welche die Ausbildung der Wachsdrüsen bei der Honigbiene beeinflussen (15.45—16.15)

Pause von 15 Minuten

G. Meyerhoff, Berlin: Instinktablauf und "Instinktirrung" beim Bienenschwarm (16.30—17.00)

F. Ruttner, Lunz Mutationen bei der Honigbiene (17.00—17.30)

H. Schmidt, Hamburg-Reinbek: Biologische Wechselbeziehungen zwischen den Termiten und den darmbewohnenden Flagellaten (17.30—18.00)

Abend frei

SAMSTAG, 11. JULI

8.30—10.45 3. Wissenschaftliche Sitzung

G. Stein, Bonn: Beiträge zur Biologie der Hummel (8.30—9.10)

F. Bausenwein, Würzburg: Zyklische Veränderungen and Drüsensystemen von Ameisen (*Formica rufa*-Gruppe) und ihr Zusammenhang mit Brutaufzucht und Kastendetermination (9.10—9.50)

W. Berwig, Würzburg: Cuticulare Stoffabgabe bei Weibchen aus der *Formica rufa*-Gruppe (9.50—10.20)

N. N. frei für Nachmeldungen (10.20—10.45)

10.45 Erfrischungspause

11.15—12.45 Einführungen zu den Demonstrationen am Nachmittag

W. Huber, Bern: Sonderausstellung "Die Biene" im Naturhistorischen Museum

A. Maurizio, Liebefeld-Bern: Papierchromatographische Untersuchungen bei Bienen

M. Lüscher, Bern: Probleme der Kastenbildung bei Termiten

13.00 Mittagessen

14.30 Stadtrundfahrt (Autobus)

15.30—18.30 Schichtweise Demonstrationen:

1. Naturhistorisches Museum. — 2. Bienenstation Liebefeld. — 3. Zoologisches Institut der Universität

19.30 Schlussbankett in Hotel "Gurten", durch die örtliche Tagungsleitung den Teilnehmern dargeboten

SONNTAG, 12. JULI

Exkursion nach Hohtenn (Wallis). Treffpunkt in der Schalterhalle des Hauptbahnhofes Bern um 6.35, Abafhrt 6.49. Rückkehr nach Bern 18.49

TRAVAUX PUBLIÉS PAR DES MEMBRES DE L'UNION

MEIDELL (O.) †: *A Terrarium to Investigate Solitary and Parasitic Bees (Hymenoptera-Apidae) in an Artificial Climate.* **Universitet i Bergen, arbok 1958. Naturvitenskapelig rekke Nr. 5, 16 pp. 6 figures,** Bergen.

An artificial terrarium is described and illustrated. Methods are mentioned for transferring the bees from the hibernaculum to the terrarium where they are exposed gradually to spring and summer temperatures. *Andrena clarkella* (Kirby) in the field confined to *Salix* blooming in April, will in the terrarium develop normal offspring in February. *Barbarea vulgaris* was used as a source of pollen. *Halictus calceatus* (Scop.) and *H. leucopus* (Kirby) are recorded as primitive social bees. *H. fratellus* Perez and *H. albipes* (Fabr.) are recorded as solitary bees. *Sphecodes crassus* Thoms. is a parasite of *H. calceatus* killing the host before laying its eggs. *Sph. hyalinatus* v. Hag. is a parasite of *H. fratellus* entering the nest while the host is in the field.

<div align="right">ASTRID LÖKEN</div>

LÖKEN (A.): *Pollination Studies in Apple Orchards of Western Norway.* **Proceedings X. International Congress of Entomology-Vol. 4, 1956 (1958)** 5 pp. 4 diagrams, 1 table, Ottawa.

The variable fruit set in Gravenstein is evaluated in relation to pollinating insects. Diagrams present the number of bumble bees, honey bees, and solitary bees in relation to temperature, sun, and precipitation records. A table showing the number of clusters under observation, bee units, per cent fruit set, etc., for each tree each year is discussed. The research indicates that the number of pollinators is not the limiting factor for the variable fruit set.

<div align="right">THE AUTHOR</div>

LÖKEN (A.): *Bombus sylvarum v. nigrescens* Pérez *new to Norway (Hymenoptera, Apidae).* **Norsk Entomologisk tidsskrift X. 1958.** 3 pp. 1 map., Oslo.

The present knowledge of the Norwegian occurrence of the melanotic variety and f. typica is given.

<div align="right">THE AUTHOR.</div>

NOTES POUR LES AUTEURS

- *Insectes sociaux* publie des mémoires originaux, des notes ou des revues concernant les problèmes relatifs aux insectes sociaux.
- Les auteurs reçoivent gratuitement 50 tirés à part.
- Les manuscrits doivent être adressés à l'un des membres du Comité de rédaction.
- Les textes remis pour l'impression doivent être dactylographiés. Leur forme sera considérée comme définitive, et leur étendue ne pourra pas dépasser 20 pages (28 lignes de 67 caractères par page) dactylographiées, illustration comprise.
- Le secrétaire se réserve le droit de demander la suppression des figures dont le nombre serait jugé excessif. Les figures au trait sont à la charge de la revue. Les planches, les photographies sont à la charge des auteurs, à l'exception de celles que le secrétaire jugerait pouvoir prendre au compte de la revue. Les documents doivent être fournis prêts à clicher.
- Les légendes des figures doivent être indépendantes des documents d'illustration.
- Chaque article doit être accompagné d'un sommaire qui en résume les points essentiels. Il sera joint une traduction de ce sommaire en deux autres langues.
- La disposition de la bibliographie doit être conforme aux règles suivantes de présentation : Date. Nom (prénom). — Titre de l'article (titre du périodique. Année. Numéro du tome, pages de début et de fin de l'article).
- Les épreuves sont adressées aux auteurs pour correction. Elles doivent être retournées SANS DÉLAI au secrétaire : G. Richard, Laboratoire de Biologie Animale, Faculté des Sciences, RENNES (I.-et-V.) — France.

SOMMAIRE